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ADAPTATION OF SORENSEN'S K (1948) FOR ESTIMATING UNIT AFFINITIES IN PRAIRIE VEGETATION[1]

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INTRODUCTION

The indigenous vegetation of Southwestern Saskatchewan has evolved under a semi-arid continental climate. Reports by Clarke *et al.* (1942) and Coupland (1958), which considered characteristics of this vegetation, classified the cover as mixed-grass prairie, following the climax concept of Weaver and Clements (1938). However, the cover is not uniform and can be classified into distinct types and sub-types by both edaphic characteristics and moisture gradients. In addition, modifications can be recognized as a result of past and present utilization.

The study being reported at this time is the result of preliminary investigations to establish a classification based on floristic similarity of sites on the basis of species presence. The methods employed follow procedures outlined by Braun-Blanquet (1951); in addition, certain mathematical concepts are introduced to estimate the probability of significant relationships between species, sample sites, or both.

PROCEDURE AND DISCUSSION

Braun-Blanquet's recommended phytosociological precedures were followed to classify 775 site lists containing 230 plant species into floristically similar units. An association table was composed to identify characteristic species; a species was considered to be "characteristic" when it occurred in at least 60% of the site lists included in the floristic unit.

However, similarity between site lists may vary in significance, as one or more of the species whose presence is less than 60% may cause variations of considerable magnitude in the total floristic composition. The significance of similarity between site lists, therefore, cannot be estimated from the association table. These considerations indicated the need for a readily tabulated statistic which would estimate the floristic similarity of sites and which could be tested for probability. Of several statistics considered, three appeared particularly useful and were tested against available data. These were: (1) The Index of Diversity -α, based on Fisher's logarithmic series and as used by Williams (1944, 1947); (2) Kendall's Rank Correlation Coefficient — T, (1948); and (3) Sorensen's Quotient of Similarity — K, (1948) which expresses the percentage similarity of two sites.

The advantages and disadvantages of each are considered.

The Index of Diversity

Williams demonstrated the application of his Index of Diversity to certain biological problems, particularly the extent of association between units and groups of insect populations according to Fisher's logarithmic series. It is applicable to studies where populations are completely randomized, and expresses the principle that in randomly distributed populations an increase in sample size will show an increase in species not encountered in the smaller sample, ad infinitum. Thus, applied to vegetation, an increasing number of samples of a particular community should show an increasing number of species occurring in only one or a few samples, while at the same time the number of species occurring in all or nearly all samples should decrease.

When applied to samples drawn from the vegetation of Southwestern Saskatchewan, the Index of Diversity demonstrated a non-random distribution of plant species, deviating from the logarithmic series especially in the number of species occurring in a large percentage of the samples, and suggesting a marked association between species in samples which had been classified as similar by phytosociological procedures. These considerations suggested that other statistics might be more useful.

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Kendall's Rank Correlation Coefficient — T

As used in this paper, the Rank Correlation Coefficient — T, is a measure of the association between two sites based on the number of species common to both sites. Its formula is presented together with a 2 x 2 reference table:

$$Tab = \frac{Cw - xy}{\sqrt{(Au)(Bv)}} \tag{1}$$

$$\begin{array}{cc|c} C & x & A \\ y & w & u \\ \hline B & v & S \end{array} \tag{2}$$

when $S =$ the number of species listed at N sites
$A =$ the number of species listed at site a
$B =$ the number of species listed at site b
$C =$ the number of species common to a and b
$u = S - A;\ v = S - B;\ x = A - C;\ y = B - C;\ w = u - y = v - x.$

The significance of any T_{ab} coefficient can be determined by the Chi^2 test when A, B and S are known. This requires the calculation of a coefficient of significance (T_e), which is a function of probability. The formulae to estimate T_e are indicated in equations 3, 4, 5 and 6:

$$\text{Chi}^2 = \frac{(Cw - xy)^2\, S}{(Au)(Bv)} \tag{3}$$

or for the purpose of this study:

$$Cw - xy = \sqrt{\frac{\text{Chi}^2\,(Au)(Bv)}{S}} \tag{4}$$

To illustrate the calculations assume that $S = 100$, A and B both equal 40, u and v each equal 60, and Chi^2 at $P = 0.001$ for 2df equals 13.82. Substitution of these values in equations (4) and (1) will estimate a T_e coefficient:

$$Cw - xy = \sqrt{\frac{13.82\,(2400)^2}{100}} = 892 \tag{5}$$

and

$$T_e = \frac{892}{\sqrt{(2400)^2}} = 0.3717 \tag{6}$$

All combinations of A and B where S equals 100 will estimate a T_e of 0.3717. Thus all T_{ab} coefficients greater than 0.3717 will indicate a significant relationship between any two sites ($P \geqq 0.001$); a smaller coefficient would indicate a lack of association between sites. However, to classify 775 sites by the T statistic, it would be necessary to calculate innumerable coefficients, because T_e has to be calculated for each successive smaller value of S and for each different combination of A and B. It is simpler to classify the sites into groups by phytosociological procedures, and test the sites within each apparent unit for similarity. Further, a more simple calculation would speed the procedure, and for this reason Sorensen's Quotient of Similarity was investigated.

Sorensen's Quotient of Similarity — K

K is a variation of Jaccard's (1902) coefficient of community. It is calculated according to the following formula:

$$K_{ab} = \frac{2C}{A + B} \times 100 \tag{7}$$

The simplicity of the calculation favors the use of K to estimate similarity of sites on the basis of species composition. Unfortunately, the distribution of K seems to be very complex and has not been worked out. Sorensen ignores this by establishing arbitrary values for similarity, and if a K_{ab} quotient is greater than the arbitrarily selected value, the sites being compared are considered similar. However, a minimum quotient for similarity might be set at 30, 50, or 70, any one of which might be as significant as the other.

Relationship Between T and K

Because T is a test to estimate the degree of deviation from expected coincidence, and K is a measure of similarity of two sites, it was postulated that a relationship existed between T and K. If this was so, then a quotient for significance (Ke) could be estimated for any K_{ab}. One more calculation is thus required, one to estimate C_e, which is the least number of species common to two sites that can be considered sociologically similar. With the illustration used previously, where $Cw - xy = 892$, C_e would equal 24.91. Thus, Ke (the lowest quotient for K_{ab} which could be considered significant when $S = 100$ and A and B both equal 40) would be obtained by substituting 24.91 for C in equation 7. The calculation is as follows:

$$Ke = \frac{24.91 \times 2}{(40 + 40)} \times 100 = 62.3 \tag{8}$$

APPLICATION AND RESULTS

Three premises were proposed to test the postulation of the T and K relationship. These were:

(1) That K is a reliable quotient to estimate the floristic similarity of two sites,

(2) That it is not justifiable to arbitrarily select a minimum value for *Ke* as Sorensen has done, but should be estimated from data, and,

(3) That significant *K* quotients can be employed to define phytosociological units.

Reliability of K

A relationship was established between *T* and *K*, and for any two populations *a* and *b* it was possible to plot *T* and *K* values against each other (Figures 1 and 2). However, when one population was replaced by a third with fewer or more species, the curve was no longer valid. This result demonstrated that *Ke* would depend on the sum of *A* and *B*. Furthermore, curves for one value of *S* were not valid at other levels, as *Ke* is also dependent on the magnitude of *S*. Therefore, an arbitrarily selected value for *Ke* can express entirely different relationships at different *S* levels even when *A* and *B* are constant.

The latter condition is illustrated in Figure 1 where *A*, *B*, and *C* are constant, but four *S* values are tested ($S = 50$, 75, 100, and 200); in addition, K_{ab} and *Ke* quotients are recorded on each curve. It will be noted that when *S* equals 50 or 75 a K_{ab} of 50 is not significant and barely so when $S = 100$. However, when *S* is increased to 200, a K_{ab} of 50 is well above *Ke*—the estimate for significance.

Thus, when the influence of the variables *A* and *B*, and *S* are recognized and calculations conducted to assess the variations introduced, *K* appears to be a satisfactory quotient to estimate similarity or dissimilarity of units of vegetation.

That it is not Justifiable to Choose Arbitrarily a Minimum Value for Ke

In most studies one would be working with a constant *S* and variables *A*, *B*, and *C*. Such would likely represent a unit of vegetation comprising several species lists. When studying data representing these conditions it was found that a single estimate of *Ke* could not be established. A fairly wide range of values had to be observed dependent on the magnitude of *A* and *B*; in turn each combination had to be tested for the significance of its quotient. The test can be done quickly by constructing a graph where curves are plotted for the highest, lowest, and a few intermediate sums of A and B (as in Figure 2); the significance of most other *A* and *B* combinations can be interpolated with a reasonable degree of accuracy.

Several *A* and *B* combinations with a constant *S* ($S = 100$) are presented in Figure 2. The

REFERENCE TABLE

WHEN			T	K ⊙	Te AT P=.001	Ke ⊗	Ce
S=	A+B=	C=					
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
50	20	10	.1667	50	.583	.7175	14.35
75	20	10	.318	50	.479	.5805	11.61
100	20	10	.375	50	.3717	.4975	9.95
200	20	10	.444	50	.263	.34	6.8

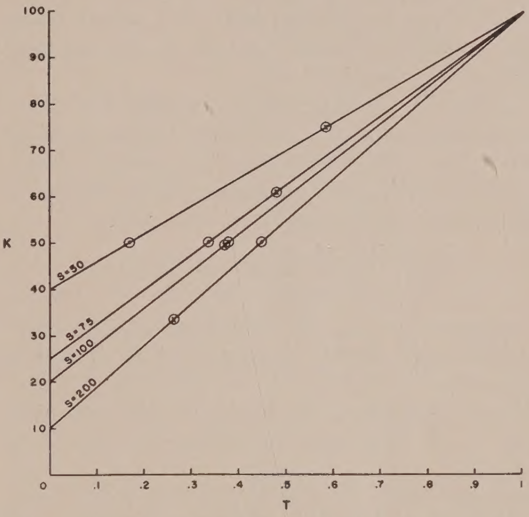

FIG. 1. Relationship between K and T with four values of S. (50, 75, 100, 200).

REFERENCE TABLE

A	B	A + B	C	S	T	K	Te ⊙/⊗	Ke	Ce
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
40	40	80	30	100	.583	75	.3717	62.3	24.19
30	40	70	21	100	.40	60	.3717	58.3	20.4
30	30	60	18	100	.285	50	.3717	56.	16.8
20	25	45	15	100	.464	60	.3717	47.2	11.8
17	40	57	17	100	.554	59.6	.3717	48.1	13.7
17	17	34	10	100	.508	58.8	.3717	48.2	8.1
20	20	40	10	100	.375	50	.3717	49.75	9.95

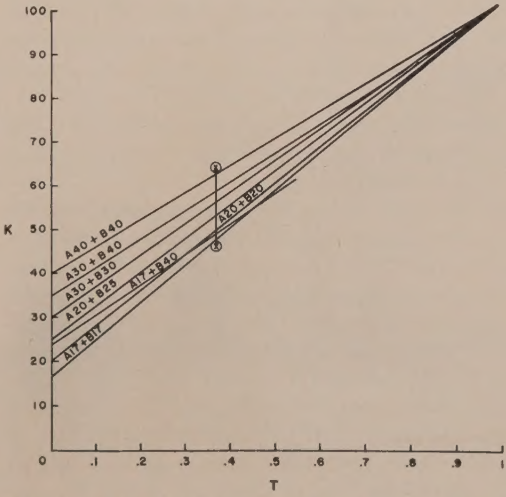

FIG. 2. Relationship between K and T when $S = 100$, and $A + B$ variable.

curves illustrate that an arbitrary selection of Ke is not justifiable despite a constant level of T_e. It will be noted that all K_{ab} quotients listed in the reference table of Figure 2 are equal to or greater than the minimum selected by Sorensen to establish his 1st Order ($K \geqq 50$), yet when the K_{ab} quotients are compared to those for Ke, one of the seven populations has a K_{ab} rating below Ke (compare columns 7 and 9 in the reference table of Figure 2).

It follows, therefore, that a value for Ke cannot be chosen arbitrarily to estimate affinity between populations. However, when a Ke quotient is estimated for each set of populations being compared, the statistic can be employed with surety.

That K Can be Employed to Define Phytosociological Units

Because there is considerable reference to Sorensen's report in the discussion which follows, a summary of his procedure to utilize the K quotient is presented. Sorensen worked with fifty lists of the vegetation of Denmark; these were compared and K_{ab} quotients for all possible combinations were calculated and tabulated. Lists, where the populations had high similarity ($K \geqq 50$), were grouped to create "Groups of the 1st Order." Groups of the 1st Order were compared with each other, and the combinations with $K \geqq 40$ were again grouped to form "Groups of the 2nd Order." Groups of the 3rd and 4th Orders were organized respectively on the basis of $K \geqq 30$ and $K \geqq 20$. With this arrangement Sorensen's 1st Order groups represented the smaller sociological units (associations and sub-associations), while his 2nd and 3rd Orders united associations into alliances and orders. The groups of his 4th Order were inconclusive and no recognized sociological unit was apparent. Thus Sorensen attempted to establish sociological units (associations, alliances, orders, and classes) by using a mathematical concept instead of arranging his lists by classical procedures.

On the other hand the precedure employed for the studies conducted in Southwestern Saskatchewan arranged site lists into "groups" by the use of association tables and employed the mathematical analyses to estimate the validity of the allocations. For each group, comprising apparently similar sites, all possible K quotients were calculated and tabulated as in Tables I and III. A value for T_e was estimated, while Ke was calculated for the greatest, least, and a few intermediate A and B sums, and plotted as in Figure 2. Thus a range of Ke values was obtained to estimate the significance of the K_{ab} quotients. This procedure has been termed an "Array" analysis to distinguish it from the "Order" of Sorensen.

One, two, or more Array analyses may be undertaken for each "group." In the analysis of the 1st Array the calculations are based on all species (S) from all sites (N), and as S is usually large, both T_e and Ke values will be relatively small. If all K quotients are greater than Ke then all sites allocated to the "group" being studied will belong to a sociological unit.

A 2nd Array analysis is then undertaken for each group. In this calculation only those sites (N) showing relationships in the 1st Array analysis and the species (S) for those sites are included. Thus, it is necessary again to calculate T_e and Ke for the highest and lowest sums of A and B; because S is smaller both T_e and Ke will be greater. If certain combinations of sites have K quotients below Ke, the sites concerned will be set aside and re-examined; if the K quotients are all greater than Ke, then all sites will be retained in the original arrangement. After 2nd Array analysis the related populations can be described, and rearrangements of all sites can be completed with confidence. Applications of the "Array" procedure follow using material drawn from Sorensen's report and with original data from Saskatchewan studies.

Data from Sorensen's Report.—In his analysis Sorensen worked with 50 plant lists ($N = 50$) comprising 226 species ($S = 226$). When these data were studied by 1st Array analysis it was determined that the lists in Sorensen's 1st Order groups "a" and "e" were related with Ke values of 35 to 45; Sorensen described "a" and "e" as belonging to the related orders Arrhenatheretalia and Molinietalia; they comprised 15 lists (N = 15) containing 113 species ($S = 113$). The lowest A and B sum between any two of the 15 lists was 62, the greatest 98. When the lists of the "a" and "e" groups were studied for similarity in 2nd Array analysis, minimum Ke values of 48.4 to 63.3 were necessary to estimate significant relationships.

Referring to Table I it is evident that only one list (#16) has doubtful relationship to the others after 1st Array analyses, but when 2nd Array affinities are studied, it is necessary to remove four lists (#16, 17, 27, and 28), as few of their K_{ab} quotients approach those necessary for estimated significance. The remaining lists form a group in which each list is related to at least three other lists and thus form a recognizable sociological unit.

TABLE I. K_{ab} Values of Plant Populations According to Population Numbers Assigned by Sorensen 1948

Plant Population Numbers															
35	26	7	5	1	2	36	31	15	13	8	17	28	16	27	Plant Population Numbers
..	61	60	56	52	54	53	57	53	43	54	47	42	38	53	35
	..	67	62	49	55	50	51	56	50	61	41	34	24	53	26
		..	81	54	57	56	51	58	49	59	50	36	30	48	7
			..	63	63	58	53	64	54	66	48	37	27	55	5
				..	72	73	52	60	55	67	55	45	35	51	1
					..	75	67	60	55	65	55	47	36	53	2
						..	63	64	56	58	57	57	45	49	36
							..	55	60	46	58	49	49	56	31
								..	61	58	49	46	38	50	15
									..	49	51	45	50	41	13
										..	50	42	27	56	8
											..	52	56	44	17
												..	54	40	28
													..	26	16
														..	27

Ke for 1st Array 35-45
Ke for 2nd Array 48.4-63.3

Characteristic species by classes, alliances, and associations listed in Sorensen's 1st Order groups "a" and "e" are presented in Table II, together with their presence ratings in the eleven population lists. These data have been compared to classifications of the vegetation of Western Europe by Westhoff *et al.* (6) and Knapp (7)[3], and it is evident from the comparison that the association can be classified as follows:

TABLE II. Characteristics (kensoorts) of the Sociological Units "a" and "e" of Sorensen wiht Constancy Percentages

Sociological Unit	Species and Percentage Constancy	
Class: Molinieto—Arrhenatheretea	Poa pratensis	100
	Festuca rubra	100
	Agrostis tenuis	100
	Plantago lanceolata	100
	Anthoxanthum odoratum	91
	Rumex acetosa	73
	Leontodon autumnalis	82
	Cerastium caespitosum	91
	Stellaria graminea	82
	Bellis perennis	73
	Potentilla reptans	55
	Trifolium dubium	46
	Trifolium pratense	36
	Polygala vulgaris	27
	Prunella vulgaris	27
	Holcus lanatus	27
	Ranunculus acer	18
	Centaurea jacea	9
	Vicia cracca	27
	Dactylis glomerata	46
	Festuca pratensis	9
	Potentilla erecta	9
Alliance: Arrhenatherion elatioris	Bromus mollis	55
	Avena pubescens	27
Association: Lolieto—Cynosuretum	Cynosurus cristatus	82
	Phleum pratense	55
	Trifolium repens	100
Sub-association: Lolieto—Cynosuretum luzuletosum campestris	Luzula campestris	100
	Hieracium pilosella	100
	Lotus corniculatus	64
	Ranunculus bulbosus	100
Class: Brometo—Corynephoretea	Achillea millefolium	100
	Festuca ovina	91
	Galium verum	82
	Cerastium semidecandrum	46
	Viola canina	46
	Campanula rotundifolia	63
	Arenaria serpyllifolia	46
	Thymus chamaedrys	36
	Hypochoeris radicata	36
	Aira praecox	36
	Carex caryophyllea	36
	Cirsium acaule	18
	Sedum acre	18
	Trifolium arvense	9
	Trifolium medium	27
	Potentilla argentea	9
	Artemisia campestris	9
	Ononis spinosa	9

Class: Molinieto-Arrhenatheretea Tx. 1937.
Alliance: Arrhenatherion elatioris (W. Koch 1926) Tx. 1937.
Association: Lolieto-Cynosuretum (Br.-Bl. et deL. 1936) Tx. 1937.

The occurrence of certain species, notably, *Luzula campestris, Hieracium pilosella* and *Ranunculus bulbosa* suggest that the unit is not the typical association but a sub-association which has been described as follows:

Sub-association: Lolieto-Cynosuretum luzuletosum campestris Tx. 1937.
Ecology: Lean pasture, on somewhat drier and poorer soils than the Lolieto-Cynosuretum typicum. On diluvial sand- and loam-soils; also on alluvial river- and dune-sand. Westhoff *et al.* (1946).

Data from Southwestern Saskatchewan—Seven hundred and seventy-five lists ($N = 775$) comprising 230 species ($S = 230$) were compiled from 1955 to 1957. These data were classified by phytosociological procedures to establish classes, orders, alliances, and associations. Twenty-three of the 775 lists were classified as follows:

Class: Astragaleto-Stipetea
Order: Astragaleto-Stipetalia comatae
Alliance: Erigonion flavi 4
Association: Astragaletum caespitosi

The 23 lists were studied by Array analyses to establish characteristics not apparent from the Association Table. K_{ab} quotients were calculated and are presented in Table III. A T_e coefficient was calculated, while Ke quotients were estimated. As all K_{ab} quotients were greater than Ke, the 1st Array analysis indicated strong relationships between the 23 sites and that the vegetational covers were

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[3] Although the classifications established by Westhoff *et al.* and Knapp are in general agreement, one author may mention local or regional characteristics which the other does not recognize for that particular unit. The classification presented in Table 2 recognizes contributions from both authors.

TABLE III. K_{ab} Values Calculated for 23 Populations Classified as association Astragaletum caespitosi of the alliance Eriogonion flavi

Group I Lists						Group II Lists						Group III Lists				Group IV Lists							Plant Lists
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	
.	86	77	78	77	68	70	79	82	83	74	73	67	68	73	62	55	57	57	50	52	52	50	1
	.	84	75	68	70	69	70	79	74	76	70	65	65	75	68	61	53	60	53	58	49	50	2
		.	91	76	73	74	68	76	67	68	69	68	68	77	67	68	53	58	55	63	49	47	3
			.	82	70	72	70	78	68	70	70	69	69	74	64	65	55	50	52	60	50	50	4
				.	83	79	73	76	72	79	77	76	72	73	71	64	60	54	53	62	58	55	5
					.	71	75	78	74	81	74	72	78	74	73	66	60	45	58	58	60	57	6
						.	81	74	80	77	84	74	75	76	74	53	59	50	52	59	60	58	7
							.	83	89	76	79	68	74	74	68	56	60	50	52	55	61	60	8
								.	85	84	82	71	77	82	71	58	50	53	58	62	53	55	9
									.	80	83	67	73	73	67	58	55	55	58	57	60	61	10
										.	80	68	70	75	68	61	65	60	53	60	58	61	11
											.	77	73	74	77	61	65	62	63	57	62	60	12
												.	92	89	80	70	55	55	64	70	58	50	13
													.	90	77	75	62	55	60	69	67	61	14
														.	82	52	62	53	58	70	55	52	15
															.	70	63	50	55	65	55	52	16
																.	70	66	79	76	71	71	17
																	.	71	70	65	78	79	18
																		.	71	65	65	66	19
																			.	81	68	67	20
																				.	73	70	21
																					.	80	22
																						.	23

Ke for 1st Array 35-43 ($S=230$)
Ke for 2nd Array 72.2-77 ($S=47$)

representative of the association Astragaletum caespitosi.

However, 2nd Array analysis ($N=23$, $S=47$) showed that K_{ab} quotients of 72.2 to 77 were necessary for significant similarity of sites. As K_{ab} quotients of the lists from 7 sites were below the required range, they were set aside from the original grouping and reclassified (Lists #17 to 23, Group 4, Tables III and IV).

The 2nd Array analysis demonstrated that further sub-division of the remaining 16 lists was possible. Consequently, three groups—I, II, and III were established according to the similarity of the sites. These groupings can be explained ecologically. Group I lists are comprised of species which characterize strongly-eroding sites where the environment provides only minimum needs for the association, while the species found in Group II lists are indicative of less severe erosion. Those of Group III are indicative of an environment near the optimum for the association, and represent an eroded form of the Festuca scabrella Association of Moss and Campbell (8). Group IV sites show little or no erosion, and could represent the last stage of the association in transition to a higher type of grassland.

As a corollary to the ecological notes, the abundance and frequency of *Astragalus caespitosus* (the indicator for the association) are stated for each of the 23 sites at the bottom of Table IV. It will be observed that its abundance increases from Groups I and III, but is negligible in Group IV.

Thus, on the basis of recognized phytosociological procedures and the Array analyses described, the 23 lists were classified as follows:

Group I. Lists 1-6, Tables III and IV.
Sub-association: Astragaletum caespitosi-Astragaletosum triphylli.
Ecology: Strongly eroded, highly calcareous soils, gravelly sandy-loam or light loam; open vegetation.
Soil Characteristics: pH 8.69; organic matter 1.23%; moisture holding capacity 40%; saturation of base exchange capacity 63%.
Groups II and III. Lists 7-16, Tables III and IV.
Association: Astragaletum caespitosi
Ecology: Eroded, highly calcareous soil, gravelly sandy-loam or light loam; open vegetation.
Soil Characteristics: pH 8.27-8.20; organic matter 3.20-3.43%; moisture holding capacity 50-56%; saturation of base exchange capacity 58-60%.
Group IV. Lists 17-23, Tables III and IV.
Sub-association: Boutelouetum gracilis-Astragaletosum caespitosi.
Ecology: Lightly to moderately eroded soils, calcareous, sandy-loam to loam; often somewhat gravelly. Vegetation discontinuous.
Soil Characteristics: pH 8.05; organic matter 4.40%; moisture holding capacity 61%; saturation of base exchange capacity 55%.

Table IV. Characteristics (kensorts) by Class, Alliance, and Association of the Association Astragaletum caespitosi

Phytosociological Units and Kensorts	Group I Lists						Group II Lists						Group III Lists				Group IV Lists						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Class and order																							
Agropyron dasystachyum	x	x			x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x
Koeleria cristata	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Stipa comata	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Artemisia frigida			x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x
Gutierrezia diversifolia	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x
Phlox hoodii	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Agropyron smithii			x	x			x																
Calamagrostis montanensis	x			x	x		x	x	x	x		x	x	x	x	x							
Comandra pallida	x	x	x	x	x		x	x	x	x	x	x		x	x	x	x	x			x	x	x
Erigeron caespitosus	x	x	x				x	x	x	x		x	x	x	x	x			x	x	x		
Petalostemon purpureus					x														x	x	x		
Linum lewissi	x		x	x	x	x		x	x				x	x	x		x						
Chrysopsis villosa									x		x	x					x	x	x	x	x	x	x
Alliance: *Eriogonion flavi*																							
Eriogonum flavum	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Haplopappus nuttallii	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x								
Oxytropis macounii		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x						
Oreocarya glomerata	x			x	x	x	x	x		x	x	x	x	x				x				x	x
Hymenoxys richardsonii	x	x		x			x	x	x	x	x	x	x	x	x	x							
Muhlenbergia cuspidata					x	x	x					x	x	x		x	x			x	x	x	x
Carex filifolia	x	x	x	x	x	x	x	x	x	x	x	x			x	x	x	x	x				x
Artemisia camporum		x	x	x		x							x	x	x	x	x		x	x			
Lesquerella arenosa	x	x	x	x					x	x		x					x		x	x	x		
Musineon divaricatum						x	x	x	x	x	x	x	x	x	x	x							
Senecio canus	x	x	x	x	x	x			x		x		x	x	x	x	x				x		
Sub-association: Astragaletosum triphylli																							
Astragalus triphyllus			x	x	x	x																	
Pentstemon nitidus						x		x	x	x				x			x			x	x	x	x
Petalostemon candidus																	x			x	x		
Erigeron compositus																	x						
Haplopappus armerioides	x	x		x																			
Association: Astragaletum caespitosi																							
Astragalus caespitosis	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Townsendia sericea			x	x			x						x	x	x	x	x				x		
Alliance: Boutelouion gracilis																							
Bouteloua gracilis			x	x	x												x	x	x	x	x	x	x
Haplopappus spinulosus																x		x				x	x
Liatris punctata														x			x	x	x			x	x
Carex eleocharis													x	x	x	x	x	x	x	x	x	x	x
Festuca scabrella[1]													x	x	x	x	x						
Gaillardia aristata[1]													x	x	x	x	x	x		x	x		
Abundance and Frequency of Astragalus caespitosis	2.4	2.4	1.3	1.3	1.3	3.3	1.3	3.3	2.3	3.5	2.3	1.2	3.3	3.3	4.3	5.3	+.1	+.2	+.1	+.3	+.3	+.1	+.2

[1] Indication of a more developed order.

The above divisions of the association Astragaletum caespitosi were not apparent in first floristic ordering. The reclassification demonstrates the usefulness of the mathematical concepts employed, and further, follows the ecological and edaphic characteristics of the units more closely than the original grouping. It is evident that relationships estimated by K can define units of Prairie vegetation.

CONCLUSIONS

In connection with phytosociological studies conducted with indigenous vegetation in Southwestern Saskatchewan, an adaptation of Sorensen's Quotient of Similarity-K, was devised to estimate affinity between sites, according to species presence. The results of the study showed that K, as used by Sorensen, was an unsatisfactory statistic, because the probability of a quotient could not be estimated. This weakness was corrected by developing a technique based on the combined use of Kendall's Rank Correlation Coefficient-T, and Sorensen's Quotient of Similarity-K. It was concluded that the technique could be employed to (1) estimate similarity of sites—both within and between phytosociological units, (2) to group sites according to ecological characteristics with a preciseness not obtainable when only standard phytosociological procedures were employed, and (3) that the small amount of extra time required to calculate T_e and Ke was more than compensated for by the additional information obtained.

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INFESTATION OF CHYTRIDIACEOUS FUNGI ON PHYTOPLANKTON IN RELATION TO CERTAIN ENVIRONMENTAL FACTORS

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INTRODUCTION

The ecological role of the fungi in nature, particularly that of the aquatic fungi, has long been a subject for conjecture and speculation. These aquatic plants, with the bacteria and protozoa, are of great significance in the break-down of dead organic matter and in the returning of nutrient materials into the environment. The abundance and variety of aquatic fungi can be verified by microscopic examination of the silmy surface of an apple, an onion, a rose hip, or a wild cherry fruit which has been immersed for several weeks in natural waters. Kanouse (1925) states that zoospores of members of Saprolegnia, Achlya, and Pythiomorpha are probably present in most fresh water habitats. Weston (1940), who discussed the role of aquatic fungi in hydrobiology suggests that no type of inland water lacks representatives of the Phycomycetes and points out that members of practically all major groups of fresh water organisms are attacked by aquatic fungi.

The only quantitative limnological studies of aquatic Phycomycetes appear to be the investigations of Canter and Lund (1948, 1951, 1953) in the English Lake District. They found that epidemic parasitism of the chytrid *Rhizophydium planktonium* Canter on the diatom *Asterionella formosa* Hass. delays the time of algal maximum or decreases the number of diatoms present during such a period. Parasitism by fungi of one species of algae may favor the development of other phytoplankters. The degree of infection of a population depends on the relative fluctuation in the numbers of fungal and algal cells. When conditions are suitable, a parasite can increase in numbers faster than its host, as evidenced by epidemics which preceded or followed the time at which the maximum numbers of algal cells were present. Often an epidemic occurs at the time of the decline in host maximum, which may cause an appreciable ecological effect since the decline is then earlier than it otherwise would have been. Canter and Lund point out that factors such as the amount of available silica in the water and the duration and intensity of light are difficult to correlate with degree of parasitism.

This investigation was conducted at Frains Lake, Washtenaw County, Michigan, for one year. Two chytridiaceous fungi were studied. One, *Rhizosiphon anabaenae* (Rodhe and Skuja) Canter, was parasitic on the blue-green alga, *Anabaena planktonica* Brunnthaler (Fig. 1; B, C), and the other, *Amphicypellus elegans* Ingold, was saprophytic on dead thecae of the dinoflagellate, *Cera-*

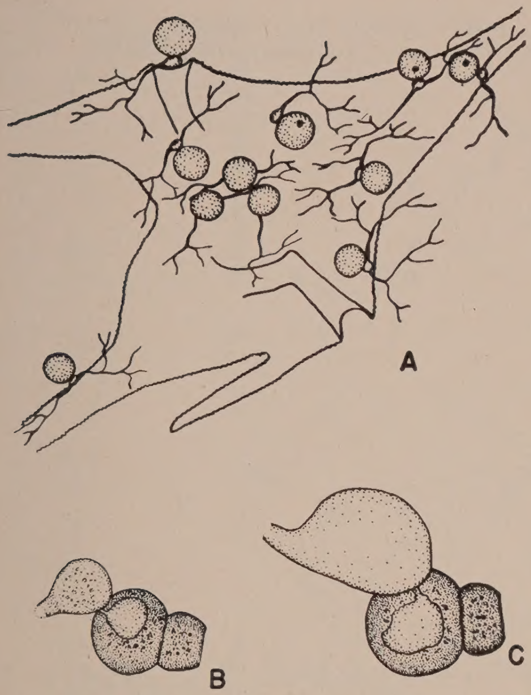

Fig. 1. A. Thalli of *Amphicypellus elegans* on dead theca of *Ceratium hirundinella*. B, C. Thalli of *Rhizosiphon anabaenae* infecting host, *Anabaena planktonica*.

tium hirundinella (O. F .M.) Schrank (Fig. 1, A). Quantitative methods were used to study the relationships of these organisms to the temperature, dissolved oxygen, hydrogen-ion concentration, and total alkalinity.

The Lake

Frains Lake is a kettle lake in Washtenaw County, Michigan (T.2S., R.7E., Sec. 9). It has a maximum depth of 9.1 m and a surface area of 67,180 sq m. The average secchi disc reading of 2 m prevailing from June, 1955, through June, 1956, reflects the low transparency of the water, which is usually yellow-green owing to the abundance of phytoplankton. The bottom is soft grey-black "ooze". The margins support an abundant growth of aquatic angiosperms, such as species of Nuphar, Elodea, Ceratophyllum, Potamogeton, and Lemna, and are densely covered with filamentous algae, notably species of Spirogyra, Cladophora, and Hydrodictyon. A further factor which influences the ecology of the lake is the excreta from livestock quartered along the southern shore. This material contributes significantly to the organic content of the water.

Methods

With few exceptions the methods employed in this investigation may be found in "Limnological Methods" (Welch 1948) or "Standard Methods for the examination of Water, Sewage, and Industrial Wastes" (American Public Health Association, et al., 1955). Preliminary investigations were conducted at Frains Lake during March, April, and May, 1954. Extensive physical, chemical, and biological sampling was started on June 15, 1955, and terminated on June 24, 1956. Sampling was done every few days at depths of 0.5 and 1.5 m, except during the winter season (October 19, 1955 to February 4, 1956) when collections were made once or twice a month at 0.5 m. A single station approximately 60 m from the north-western shore with a water depth of 4 m was used. This is a permanent, marked station utilized by the University of Michigan Zoology Department. In addition, occasional collections were made at a station close to the lake center, which has a depth of 9 m, to ascertain whether the material from the permanent station was a representative sampling of the lake.

Temperatures in degrees centigrade were measured at half-meter intervals by the Whitney electric resistance thermometer.

Samples for the chemical determinations were collected by a suction apparatus designed by Dr. George W. Saunders of the University of Michigan Zoology Department. This is similar in function to the one described by Welch (1948) as the "pump and hose method." For each water sample the following chemical measurements were made immediately in the field: (1) Oxygen, by the Pomeroy-Kirschman-Alsterberg modification of the Winkler method in ppm; (2) Hydrogen-ion concentration, by the Beckman pH meter; (3) Total alkalinity, by the Beckman pH meter. Sulfuric acid, 0.01 N, was added until the pH was 4.0. This is the pH recommended by Welch (1948) when substituting other indicator methods for methyl orange. Carbonate and HCO_2 were determined from the total alkalinity and pH by the method of Moore (1939).

Plankton collections were made with a two liter Kemmerer sampler at depths of 0.5 and 1.5 m. The water samples were placed in half-gallon jugs and formalin was added to make a 5% solution. Later, 5, 10, 25, or 50 cc subsamples were placed in Utermöhl sedimentation chambers for 24 hr. To induce settling of blue-green algae a fatty acid detergent, "Tergitol" Penetrant 7, a trademark product of the Union Carbide and Carbon Corporation, was added.

Filaments and cells of *Anabaena planktonica*, cells of *Ceratium hirundinella*, and thalli of *Rhizosiphon anabaenae* and *Amphicypellus elegans* were

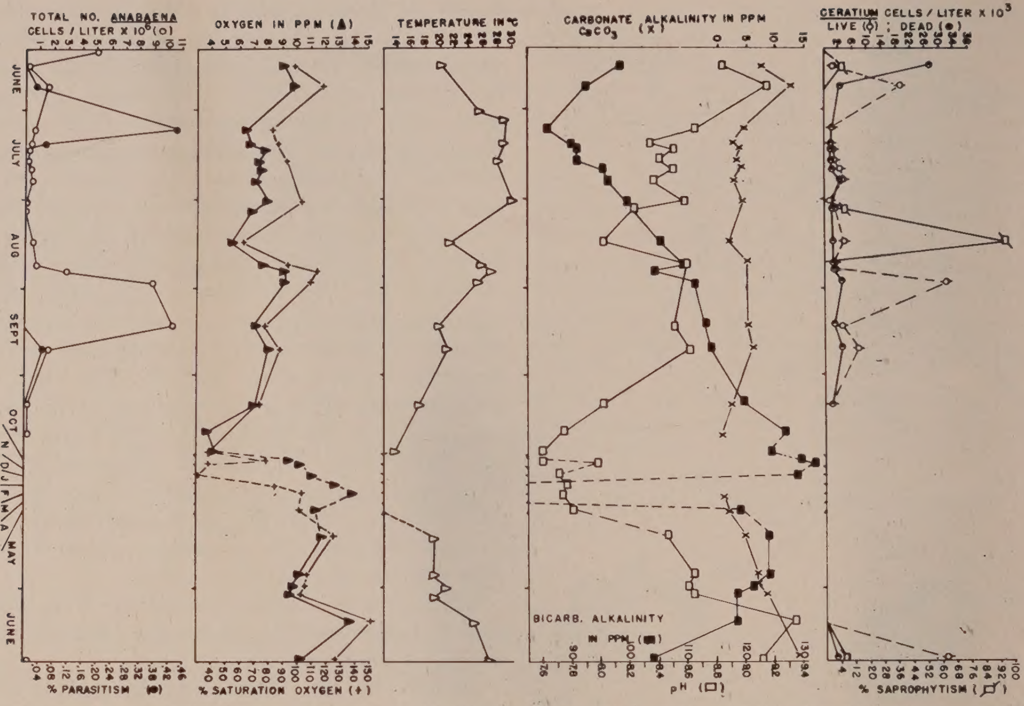

Fig. 2. Seasonal distribution of *Anabaena planktonica, Rhizosiphon anabaenae, Ceratium hirundinella, Amphicypellus elegans,* temperature, dissolved oxygen, hydrogen-ion concentration, carbonate and bicarbonate alkalinity at 0.5 m in Frains Lake from June 10, 1955-June 24, 1956.

counted by the inverted microscope technique of Utermöhl (1931). Duplicate samples from each level were counted to at least 100 cells and filaments. Total counts (often 600-700 cells) were made of *Ceratia* in each subsample. For Anabaena all cells in 100 filaments were counted. All filaments of Anabaena were counted .

Physical-Chemical Data

Temperature

From the second week in December, 1955, until the middle of March, 1956, the surface of Frains Lake was covered with ice. The maximum thickness of the ice, 9 in. (0.23 m), was on December 31, 1955. Snow was frequently present on the frozen surface and on February 4, 1956, the snow layer was 4 in. (0.1 m) thick. Ice and snow sheets were also observed during the winter months from 1952-1955.

The winter temperature under the ice averaged 3°C at 0.5 m. Following the spring breakup and melting of the ice there was a temperature rise of the lake water at 0.5 and 1.5 m. The seasonal variation in temperature at those levels is shown in Figures 2 and 3. Water temperature increased from 3.1°C on March 3 at both levels to 26.5°C and 25.6°C at 0.5 and 1.5 m respectively on June 24, 1956. In addition, an increase was observed from 20.3°C and 19.2°C at the surface and 1.5 m respectively on June 15, 1955 to 30.1°C and 29.2°C at 0.5 and 1.5 m on August 1, 1955. The general increase in temperature was due to the increase in solar radiation during this period. Chandler and Weeks (1945) found that a seasonal increase in solar radiation at Put-in-Bay, Lake Erie, Ohio, began in early February and continued to the summer maximum in July. Irregularities of temperature shown in the graphs (Figs. 2 and 3) during this time are normal changes due to variations in meteorological conditions. Prolonged periods of cloudiness usually preceded decreases in the temperatures. Thus, overcast weather from August 1-15 may have accounted for the decrease in temperature prior to August 15. It is possible, however, that minor changes resulted from diurnal fluctuation and water movements.

Dissolved Oxygen

The seasonal distribution of dissolved oxygen, expressed in parts per million, and per cent saturation is shown in Figures 2 and 3. Per cent saturation has been used to express dissolved oxygen to separate the biological effect from the physical effect of temperature.

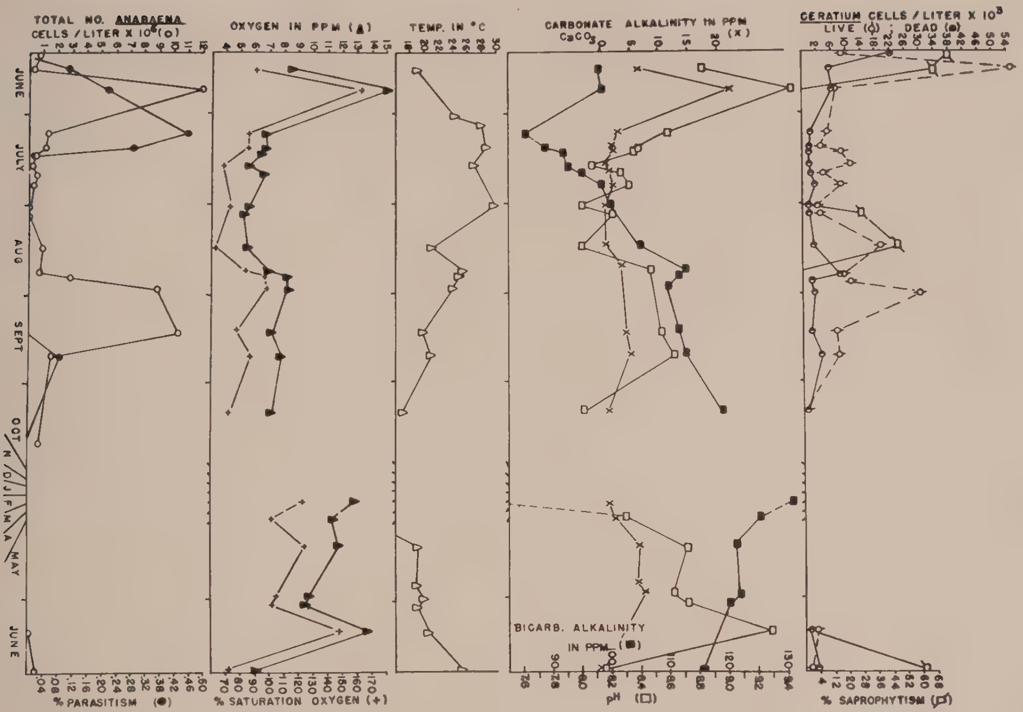

FIG. 3. Seasonal distribution of *Anabaena planktonica, Rhizosiphon anabaenae, Ceratium hirundinella, Amphicypellus elegans,* temperature, dissolved oxygen, hydrogen-ion concentration, carbonate and bicarbonate alkalinity at 1.5 m in Frains Lake from June 10, 1955-June 24, 1956.

As the graphs indicate, a simultaneous increase in number of the two dominant algal species, *Anabaena planktonica* and *Ceratium hirundinella,* occurred in June and in August and September, 1955. During these months the rise in number of Anabaena and Ceratium was coincident with the increase in dissolved oxygen. However, the June, 1956, rise in dissolved oxygen was not accompanied by a bloom of phytoplankton. At this time there was a large population of *Spirogyra* sp. in Frains Lake. It is probable that the photosynthetic activities of the phytoplankton accounted for the increase in oxygen during June and August, 1955, while the same process carried on by the Spirogyra population was responsible for the oxygen increase of June, 1956. Of the two primary sources of oxygen, atmosphere and aquatic plants, Juday and Birge (1932) regard the former as the more important. However, they found that in several Wisconsin Lakes considerable amounts of oxygen were due to photosynthetic activity.

On October 19, 1955, there was a sudden decrease in dissolved oxygen followed by a large increase during the November and December turn over period. The increase was expected since the stirring which occurs during the turn over period oxygenated the water. The decrease may perhaps be explained by the fact that strong winds prevailed during most of the week following October 10, 1955. Some hypolimnial oxygen-deficient water may have mixed with that from the epilimnion. Such mixing due to storms has been described in Waskesiu Lake, Saskatchewan, by Rawson (1936). It is possible, however, that this decline could be caused by an increase in decomposition.

Alkalinity and pH

The graphs in Figures 2 and 3 reveal that an increase in pH and carbonate alkalinity coincided with the spring and fall blooms of Anabaena and Ceratium in June and September, 1955. Since these organisms were photosynthesizing, the removal of CO_2 would be expected to increase the pH and carbonate alkalinity. It was pointed out by Juday, et al. (1935) that the large amount of literature published from 1925 to 1935 on hydrogen ion investigations showed that changes in pH and alkalinity are brought about primarily through biological processes.

Following the decline in numbers of *Anabaena planktonica* and *Ceratium hirundinella* on June 22, 1955, there was a decrease in pH and carbonate alkalinity. After June 22 there was a general leveling off of the two which continued through the summer, except on August 1, at 1.5 m and on August 16, at 0.5 and 1.5 m when there was a slight decrease in pH. This decline may be caused by the large population of zooplankton present at the time. The respiration of such animals would tend to increase the carbon dioxide content of the water, thus decreasing the pH.

There was a decrease in pH from 8.5 at 0.5 m on September 13, to 7.6 on November 10, 1955. In addition, a decline in carbonate alkalinity occurred during this period. The autumnal decrease in temperature probably accounted for an increase of carbon dioxide in the water, which in turn decreased the pH and carbonate.

Bicarbonate alkalinity showed a somewhat different pattern after the initial decrease following the Anabaena-Ceratium bloom. Figure 2 shows a steady increase in bicarbonate alkalinity from 85 ppm calcium carbonate on July 7, to a maximum of 129 ppm on December 31. A similar condition was found by Hutchinson (1941) in Lindsey Pond, Connecticut. He attributes the increase to a build up of cations in the water and to the fact that it is possible for the bicarbonate to be in balance with these ions.

BIOLOGICAL DATA

Algae

From June 10 to October 10, 1955, *Anabaena planktonica* Brunnthaler and *Ceratium hirundinella* (O. F. M.) Schrank were the dominant phytoplankton species in Frains Lake.

At the 0.5 m level there were two annual maxima in numbers of Anabaena cells, one in early June and the other from late August through the middle of September, 1955 (Fig. 2). Furthermore, indications of spring maxima were found on June 24, 1956, and in May and early June, 1954. There was a slight difference in the spring maximum between the 0.5 and 1.5 m depth. The Anabaena bloom in the deeper water occurred somewhat later than at the 0.5 m level.

Two annual maxima in the number of *Ceratium hirundinella* cells were found at depths of 0.5 and 1.5 m, one in June and the other in August and September, 1955. The beginning of a spring maximum was also found on June 24, 1956, and in May, 1954.

Fungi

The chytridiaceous parasite *Rhizosiphon anabaenae* (Rodhe and Skuja) Canter (Fig. 1, B, C) occurred in Frains Lake during the spring and autumn of 1955, during the maximum spring and fall blooms of its host, *Anabaena planktonica.* In terms of percentage of infection, which is the per cent of individual Anabaena cells infected with *Rhizosiphon anabaenae,* it was most abundant during the decline of the Anabaena population.

Amphicypellus elegans Ingold (Fig. 1, A), a chytridiaceous saprophyte, occurred at its maximum in Frains Lake during the spring and autumn of 1955 and in the spring of 1956. It was undoubtedly saprophytic on *Ceratium hirundinella,* since it was found only on dead thecae of the dinoflagellate. No correlations can be made between the occurrence of the saprophyte and the number of living Ceratium cells since the saprophytic maximum either precedes or follows the maximum for Ceratium. The only relationships observed between the number of dead Ceratium cells and *Amphicypellus elegans* were on June 10, 1955, at 1.5 m and on June 15, 1955, at 0.5 m when the maxima of dead cells coincided with the saprophyte maxima (Figs. 2 and 3).

DISCUSSION

Algal Periodicity

The occurrence of spring and autumn blooms of *Anabaena planktonica* is characteristic of most planktonic algae. Birge and Juday (1922) found such spring and autumn maxima for species of Anabaena during 1911, in Lake Mendota, Wisconsin, although in 1913, 1916, and 1917, only a late summer or autumn maximum was present. The lack of spring blooms in Lake Mendota in the latter years is explained by the fact that there was a high content of organic matter in the autumn whereas in 1911, there was a large amount of organic material in both the spring and autumn. Such influences of organic substances on blooms of blue-green algae are discussed by Hutchinson (1944) who states that this phenomenon does not occur until there is a depletion of mineral nutrients with a concomitant large increase in organic matter, which occurs usually in late summer and autumn. Pearsall (1932) found in England a clear correlation between high organic matter and maximum abundance of blue-green algae. It is reasonable to assume that the organic matter in Frains Lake is constantly high due to the quartering of animals on the entire southern shore. This undoubtedly accounts for the uncommon spring maximum of *Anabaena planktonica* in Frains Lake and also influences the expected autumn maximum of the blue-green alga.

A striking difference was observed in the time of the spring Anabaena-Ceratium maximum at 0.5 and 1.5 m (Figs. 2 and 3). The maximum at the lower depth occurred later than that at the higher level. The autumn maximum however, occurred at the same time at both depths. This spring-autumn difference is explained by temperature change. The specific gravity of many blue-green algae is reduced by a fatty oil or by "gas vacuoles" in the protoplasm. This puts the algae in such delicate balance with the water that, in stratified lakes, as pointed out by Ruttner (1953), they may sink through the epilimnion, yet remain suspended within or below the colder thermocline. In this study the spring bloom at 0.5 m occurred when the temperature is undoubtedly below 20°C which was before June 10, 1955. From June 15 to July 4 the temperature increased 8.7°C at 0.5 m and 8.5°C at 1.5 m; the temperatures on June 15 were 20.3 and 19.0°C for 0.5 and 1.5 m levels, respectively. Coincident with this, the number of Anabaena cells decreased at 0.5 m from 5 million cells per liter on June 10, to six hundred thousand cells per liter on July 7 (Fig. 2). But at 1.5 m the number of cells increased from three hundred thousand cells per liter on July 15 to a maximum of 12 million cells per liter on July 22. The increase in cells at 1.5 m and the decrease at 0.5 m were thus accounted for by a sinking of Anabaena filaments. Such settling was probably due to a change in the balance between the specific gravity of the water and that of the Anabaena protoplasm caused by an increase in the temperature of the lake. The fall bloom remained essentially the same at both levels; again temperature appeared to be the factor involved. Not only was a thermocline established from August 25-29 at 0.5 m but the temperature dropped from 27°C on August 25 at 0.5 m and 24.98°C at 1.5 to 19°C at both levels on September 13. Thus, the raising of the specific gravity of water due to a lowering of temperature caused the Anabaena filaments to remain in at least the upper 1.5 m of the lake.

A decline in the Anabaena population which ended the spring and autumn maxima probably also depended on temperature. Although it is possible that the algal filaments continued to sink below 1.5 m, thus accounting for the decline, this was not the case in the termination of the fall maximum since the alga apparently does not sink. It was possible that this decline was due to a physiological factor related to temperature. During the spring maximum there was a rise in temperature at 1.5 m from 19.2°C on June 15, at the beginning of the bloom, to 28.6°C at the end of the maximum. Furthermore, the temperature fell from 24.98°C on August 25 to 16.78°C on October 10 during the autumn bloom. The graph (Fig. 2) shows that the temperature at the height of both blooms was approximately 20 to 21°C suggesting this range as an optimum growing temperature for Anabaena. Thus, as the spring temperature rose above the optimum, the numbers of Anabaena cells diminished, perhaps through death, and as the autumn temperature fell below the same optimum there was also a population decline.

Anabaena planktonica and *Ceratium hirundinella* were the dominant phytoplankton in Frains Lake from June 10 to October 10, 1955. At 0.5 and 1.5 m there were two annual maxima in numbers of Ceratium cells, one in June and the other in August and September, 1955 (Figs. 2 and 3). Furthermore, the beginning of a spring maximum was found on June 24, 1956, and in May, 1954. The occurrence of such spring and autumn maxima in this study is characteristic of Ceratium. Birge and Juday (1922) found spring and autumn maxima for Ceratium in Lake Mendota during 1911, 1912, and 1915. Ruttner (1953) in his investigation of Lunzer Untersee in Austria reports that Ceratium has annual spring and autumn maxima which occur during the same months year after year. That the two variations are possibly a result of temperature fluctuations has been discussed in connection with the periodicity of *Anabaena planktonica*. Figures 2 and 3 show that the temperature range at both 0.5 and 1.5 m during a Ceratium maximum is between 24 and 26.5°C, with the temperature either increasing or decreasing, before or after a maximum. An exception is the apparent low temperature of 19.2°C at 1.5 m on June 15, 1955.

Fungal Periodicity

Parasite—host relationships—Figures 2 and 3 show the total number Anabaena cells and the percentage of this sum which were parasitized by Rhizosiphon at 0.5 and 1.5 m in Frains Lake. Examination of data at 0.5 m (Fig. 2) shows that on the first date of sampling, June 10, 1955, there were 5,062 x 10^3 Anabaena cells, declining to 215 x 10^3 on June 15. During this period there was no parasitism by Rhizosiphon. With an increase of host cells on June 22, the percentage of cells infected was .026. As the Anabaena cells declined in number from this June 22 peak of 1,602 x 10^3 cells to 627 x 10^3 on July 7 the percentage of cells infected increased to a maximum of 0.44% on July 7. The graphs at 1.5 m (Fig. 3) present a similar situation except that the magnitude of the June 22 Anabaena maximum was much greater. The maximum percentage of parasitism occurs during the decline of the host cells. The difference in the Anabaena maxima at the two levels has been discussed.

In autumn a similar relationship occurs. At the height of the Anabaena population, between August 29 and September 13, 1955, no parasitism was observed on 1,394 filaments from 0.5 m and 1,823 filaments from 1.5 m collected on August 29, or on 1,142 filaments from 0.5 m and 1,012 filaments from 1.5 m collected on September 13. During the decline in numbers of the blue-green alga on September 21 the maximum number of host cells was parasitized: .043% at 0.5 m and .083% at 1.5 m.

In 1949, Canter and Lund (1951) found that the percentage of parasitism of filaments of *Oscillatoria agardhii* var. *isothrix* Skuja in Esthwaite Water, England, coincided with a decline in numbers of the host filaments. This blue-green alga was parasitized by the chytridiaceous fungus, *Rhizophydium megarrhizun* Sparrow, from April 20 to May 15, 1949. These workers suggested that such a population decline in Oscillatoria may be due to environmental factors. They state, however, that the fungus also hastened the reduction in numbers of the host alga. The maximum percentage of parasitism by *Rhizophydium megarrhizum* was 43% of the Oscillatoria filaments. In this investigation it seems improbable that the infection by Rhizosiphon could appreciably hasten the decline of the Anabaena population. At the height of Rhizosiphon parasitism in Frains Lake, 13% of the filaments were infected (0.44% cells infected). The data of Canter and Lund are not comparable with that of the present study due primarily to the difference in morphology of the two parasites. The rhizoids of *Rhizophydium megarrhizum* penetrate many host cells of a filament but the entire thallus of Rhizosiphon occupies only a single cell. Furthermore, the percentage of parasitism in this investigation was never as great as that reported by Canter and Lund. The highest incidence of infection recorded here was 6% of the filaments (0.46% of the cells) of Anabaena. This could not be compared to the severe 43% infected filaments found by Canter and Lund (1951) in the parasitism of Oscillatoria by *Rhizophydium megarrhizum*.

As discussed previously, phytoplankton maxima occur in the spring and autumn. Following each maxima there is a decline in their numbers. Hutchinson (1944) discussed the causes of these declines. He gave evidence that a depletion of mineral substances is one of the major causes for such decreases in algal population. Therefore, the senility of the declining population due to physical-chemical causes is more likely to permit parasitism than for the parasite to initiate or even hasten the decline of the algal population. Canter and Lund (1948) usually found concentrations of nitrate, silica and phosphate high or rising during periods of epidemic parasitism by *Rhizophydium planktonicum* on the diatom *Asterionella formosa*. But they also noted that parasitism of Asterionella could occur in low percentages when inorganic matter was low. Parasitism was always in epidemic proportions, often up to 80 and 90% of the cells examined by Canter and Lund but in the present investigation the maximum was only 0.46%.

Parasite—dissolved oxygen relationship—Sparrow (1943) has emphasized the importance of a delicate balance between aquatic fungi and the environment. In this investigation dissolved oxygen was correlated with parasitism by *Rhizosiphon anabaenae*. As the graphs indicate, the maximum number of parasites was present during the decline in oxygen maximum. On July 7, the parasite maximum occurred when the dissolved oxygen was 82 and 85% saturated (6.4 and 6.8 ppm) at 0.5 and 1.5 m respectively, and on September 21 when it was 77% saturated (8.0 and 7.8 ppm) at 0.5 and 1.5 m. It is possible during these periods that the oxygen range of 6.4 to 8.0 ppm is the optimum for growth, development, and reproduction of the parasite. Whether such limits in parts per million of oxygen are necessary for infection cannot be demonstrated from the present data.

Parasite—pH and alkalinity relationship—During the maximum percentage of parasitism the pH in both spring and autumn fell within a range of 8.59 to 8.67 at both 0.5 and 1.5 m (Figs. 2 and 3). Hydrogen ion concentration may be a limiting factor in the parasitism of *Anabaena* by *Rhizosiphon* during these periods. The graphs also show a decrease in the pH and carbonate alkalinity during the periods of maximum percentage of parasitism. This indicates an increase in carbon dioxide during these times, which is expected, since the numbers of photosynthesizing organisms is decreasing. Such an increase in carbon dioxide may be a factor in the occurrence of parasitism.

In contrast to pH and carbonate, the bicarbonate alkalinity is quite different during the spring and autumn *Rhizosiphon* maxima. The bicarbonate alkalinity (Figs. 2 and 3), increased considerably after the autumn parasite maximum. The seasonal distribution of bicarbonate alkalinity has been discussed. During the spring Rhizosiphon maximum, on July 7, the bicarbonate alkalinity was 85 ppm at 0.5 and 1.5 m, whereas on

September 21, during the autumn maximum, it was 116 and 114 ppm at 0.5 and 1.5 m, respectively. Thus, there is apparently little relationship between alkalinity and parasitism of *Anabaena planktonica* by *Rhizosiphon anabaenae*.

Parasite—temperature relationship — Correlations of temperature to the host and to chemical factors indicate that temperature is an indirect factor with respect to degree of parasitism since it influences both biological and chemical factors. Concerning a direct relationship, the fungus seems tolerant of a wide range of temperature: during the spring parasite maxima the temperature is 29°C at 0.5 and 1.5 m, and in the autumn it is 21°C at both levels. Wide temperature tolerations were also found in *Rhizophydium planktonicum* by Canter and Lund (1948).

Saprophyte relationships—There are no limnomycological investigations known of a fungus invading a non-living component of the plankton. Therefore, there is much to be learned of the significance of this relationship. In this study, no correlation could be made between the percentage of dead *Ceratium hirundinella* cells infected with *Amphicypellus elegans* and the number of either living or dead *Ceratium* cells. The reason may be that the sampling of dead cells of the dinoflagellate was not adequate. Complete vertical sampling of the water and examination of bottom sediments might yield more accurate results, since the dead cells would be more inclined to sink than the live ones. This is a problem for future study.

Saprophyte—physical-chemical relationships—As shown in Figures 2 and 3, there is little relationship between pH, alkalinity and maximum saprophytism. However, there are recognizable correlations between temperature, dissolved oxygen, and Amphicypellus maxima. The temperature at the peak of the saprophyte maxima rose or fell between 19.2 and 21.5°C before or after a maximum. This might indicate that such a temperature range is optimum for *Amphicypellus elegans,* and that temperature is limiting above or below this range. Although dissolved oxygen does not appear to be limiting, since it had the wide range of 5.2 to 10.3 ppm (60 to 126% saturation) at both levels during the periods of saprophyte maxima, the graphs (Figs. 2 and 3) indicate a distinct drop in dissolved oxygen during these periods. This suggests that a lowering of oxygen content in the water influences the increase in numbers of *Amphicypellus elegans* on *Ceratium hirundinella.*

The complexity of physical, chemical and biological factors in the particular lacustrine habitat investigated make the study of interrelationships between the environment and parasitism very difficult. This study shows trends in factors which may indicate relationships. Additional laboratory and field studies of chytridiaceous parasites should be made.

SUMMARY

The relationships between parasite, host, and physical-chemical factors can be summarized as follows:

The percentage of parasitism of *Anabaena planktonica* by *Rhizosiphon anabaenae* occurred in two maxima during 1955. These maxima took place during the decline of the Anabaena spring and autumn blooms. Results of this investigation, in contrast to those described by Canter and Lund (1948, 1951, 1953) in their work on English lakes, indicate that parasitism does not hasten the algal decline. Rather, there are strong indications that decline in Anabaena cells is caused by environmental physical-chemical factors, not by parasitism. The senility of the declining population due to these causes is more likely to permit parasitism than for the parasite to initiate or hasten the decline or the algal population.

The maxima of *Rhizosiphon anabaenae* occurred within 6.4 to 8.0 ppm (77 to 82% saturation) of dissolved oxygen. This may indicate that oxygen is a limiting factor and that the parasite may require an optimum dissolved oxygen concentration between 6.4 to 8.0 ppm.

The spring and autumn maxima of *Rhizosiphon anabaenae* ranged in pH from 8.59 to 8.67, suggesting that an optimum pH exists for the parasite during its infection of *Anabaena planktonica.*

A decrease in pH and carbonate alkalinity indicated an increase in carbon dioxide during the Rhizosiphon maxima. This decrease may be a factor in the occurrence of parasitism. Bicarbonate alkalinity apparently has little direct effect on the parasitism of *Anabaena planktonica* by *Rhizosiphon anabaenae.*

Temperature appears to have little direct effect on the Rhizosiphon maxima, thus confirming temperature studies by Canter and Lund (1948, 1951, 1953).

The percentage of saprophytism showed no correlation with the numbers of either living or dead cells of *Ceratium hirundinella.* The sampling of the dead Ceratium cells may not have been adequate; a more complete examination of vertical water collections and bottom samples is desirable.

The maxima of *Amphicypellus elegans* occurred within a temperature range of 2.5°C indicating that there may be an optimum temperature for

Amphicypellus and that temperatures below 19°C and above 21.5°C are limiting.

Distinct drops in the dissolved oxygen content of the water occurred during the saprophyte maxima. But oxygen appeared not to be a limiting factor since it ranged from 5.2 to 10.3 ppm (60 to 126% saturation) during the peaks of saprophyte maxima. Nevertheless, a lowering of the dissolved oxygen may have influenced the increase in numbers of saprophytes.

No correlations could be made between hydrogen-ion concentration, alkalinity, and percentage of saprophytism.

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QUANTITATIVE OBSERVATIONS ON EPIDENDRIC LICHENS USED AS FOOD BY CARIBOU.[1]

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Caribou, *Rangifer arcticus* (Richardson), in Wells Gray Park (lat. 52°N., long. 120° W.), British Columbia, eat epidendric lichens of the genus Alectoria Ach. in winter. During winter these lichens provide most of their food (Edwards and Ritcey 1960), and appear to be the only food available in quantity. Survival of caribou in this area, therefore, depends in part upon the availability of Alectoria in winter. This study was undertaken to explore how much Alectoria is in the park, and the proportion of its total stand available to caribou. Partial answers to these questions are basic to determining the forest management best suited to perpetuate caribou.

Intensive field work was done in the summer of 1957. More general observations were made since 1952 when it was first apparent that arboreal lichens were an important caribou food.

There appear to be 5 species of the genus Alectoria in the park. The following nomenclature is taken from Howard (1950). One, *Alectoria sarmentosa* Ach., is light green in color. The remaining 4 (*A. fremontii* Tuck; *A. oregona* Tuck; *A. chalybeiformis* (L.) Rohl; *A. jubata* (L.) Ach.) are dark brown. The last 3 are difficult to separate in the field. In this study these are considered together as the *Alectoria jubata* complex, and any reference to this species is meant to indicate the complex.

These plants consist of linear, threadlike filaments which branch dichotomously and decrease in diameter distally. Aggregations of finer threads resemble coarse hair. They may occur luxuriantly on branches and foliage of trees; some species are predominantly pendulous, others are prostrate and form tangled masses among twigs and needles.

METHODS

We chose for study 4 tenth-acre areas in 4 kinds of forest. Within each study area 11 to 13 trees were chosen by a forester (Soos) as representative, in aggregate, of the forest type. From these, within each successive 10 ft height interval, 2 representative branches were arbitrarily selected. From each branch all Alectoria was removed by hand, the species composition estimated in percentages by volume, and the mass of lichen then oven-dried and weighed. Collecting lichen from the branches of one large tree involved hours of work to separate fine strands of lichen from bark, twigs and foliage.

STUDY AREAS

Areas 1 and 2 were in a region not frequented by caribou. They were chosen for their accessibility and suitability for perfecting techniques and gathering ecological data on lichens. Areas 3 and 4 were in regions regularly frequented by caribou, the former on the valley floor, the latter near timberline.

Area 1, at 2600 ft., had an uneven aged stand of mixed conifers at the edge of a 20 year old burn. Most trees were 80 to 130 years old. Douglas fir (*Pseudotsuga menziesii*) was dominant, Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) the most numerous co-dominants. Regeneration, predominantly cedar (*Thuja plicata*), was common where fallen trees had opened the stand. Seventy per cent of the forest floor was covered by mosses. Most common herbs were *Linnaea borealis, Cornus canadensis* and *Clintonia uniflora*. Deciduous shrubs were scarce except for some scattered *Pachistima myrsinites*. This area was centrally located on the floor of a broad valley.

Area 2, at 2600 ft, had an even aged stand of mixed lodgepole pine (*Pinus contorta*), Douglas fir, trembling aspen (*Populus tremuloides*), Engelmann spruce, subalpine fir and paper birch (*Betula papyrifera*). Most trees were 50 to 60 years old. Spruce regeneration was common where the intolerant aspen and willows had died. The shrub layer was low and composed of *Rosa* spp., *Shepherdia canadensis, Spirea lucida, Rubus parviflorus, Juniperus communis,* and *Vaccinium membranaceum*. Common herbs were *Cornus canadensis, Linnaea borealis, Chimaphila umbellata, Aralia nudicaulis,* and *Pyrola secunda*.

Area 3, at 3700 ft, was in a mature stand of Engelmann spruce and subalpine fir opened by selective cutting 20 years before. Most trees were 150 to 180 years old with dominants 90 to 120 ft high. Regeneration was mainly spruce and subalpine fir, with some cedar and hemlock (*Tsuga heterophylla*). There was a moderately dense shrub layer, dominated by *Menziesia ferruginea*, with *Lonicera involucrata, Rubus parviflorus, Oplopanax horridus,* and *Ribes* spp. Ground flora was dominated by oak fern (*Gymnocarpium dryopteris*) in July, with *Linnaea borealis, Cornus canadensis, Rubus pedatus, Tiarella unifoliata, Aralia nudicaulis, Clintonia uniflora* and *Lycopodium* sp. This area was in a narrow valley and part of an extensive tract of mature forest. Precipitation is heavier than in Areas 1 and 2. Caribou frequent this area in fall, winter and spring.

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Area 4 was near 6000 ft. Here a mature stand of Engelmann spruce and subalpine fir had a shrubby understory composed almost entirely of regenerating spruce and fir. This low growth was almost impenetrable at the forest edge adjacent to natural timberline meadows. The main deciduous shrub was *Vaccinium caespitosum*. Ground cover, chiefly mosses with a few lichens, was sparse. Openings and edges had a variety of herbs and dwarf shrubs, among them *Phyllodoce empetriformis, Luetkea pectinata, Veratrum eschscholtzii,* and *Arnica latifolia*. This area, near timberline, has snow depths up to 7 ft in late winter.

TOTAL WEIGHTS OF ALECTORIA

Total weights in kg. per acre for the 4 study areas appear in Table I. Area 4 was by far the heaviest producer. Alectoria when dried seems light in weight, yet this area had nearly 1.5 tons per acre. This confirms casual observation that timberline forests in this region have heaviest stands of lichen.

TABLE I. Weights of lichen, Alectoria, on study areas

Study Area	Kilograms of lichen per acre	KILOGRAMS PER ACRE AND PER CENT OF TOTAL LICHEN BELOW THREE HEIGHTS FROM GROUND		
		10 ft	15 ft	20 ft
1......	339.2	5.5 (2%)	51.5 (14%)	89.1 (24%)
2......	114.4	11.0 (10%)	27.7 (24%)	44.5 (39%)
3......	305.9	26.1 (9%)	56.2 (18%)	128.2 (42%)
4......	1,332.0	169.6 (13%)	329.2 (24%)	456.7 (34%)

The relatively young forest, mainly of lodgepole pine, in Area 2 had the lightest stands of lichen. Alectoria is a common genus on pines in the region and seems especially common on pines in boggy areas. However, if Area 2 is typical, lichen loads are not heavy. Perhaps a false impression of abundance results from the lichen being easily visible in the open crowns of these trees.

Originally we thought that Area 3 had a heavier stand of lichen than Area 1. Data show the reverse is true, although the figures suggest no great difference. These figures are from restricted areas, however, and further sampling might confirm our original opinion.

THE VERTICAL DISTRIBUTION OF ALECTORIA

A meaningful picture of lichen loads on trees must include some indication of vertical distribution. Feeding caribou would derive little benefit from a lichen abundance of a ton per acre if it was confined to the tops of tall trees. To investigate vertical distribution, lichen loads in each study area were calculated for successive 10 ft intervals from the ground. These data appear in Figure 1 for the species of Alectoria treated collectively, and in Figure 2 for each species separately. Patterns of distribution are the result of several factors controlling abundance. It is a temptation to regard them solely as reflections of microclimate affecting lichen growth. The figures may be valuable from this viewpoint, but there are additional controls on abundance which complicate analyses.

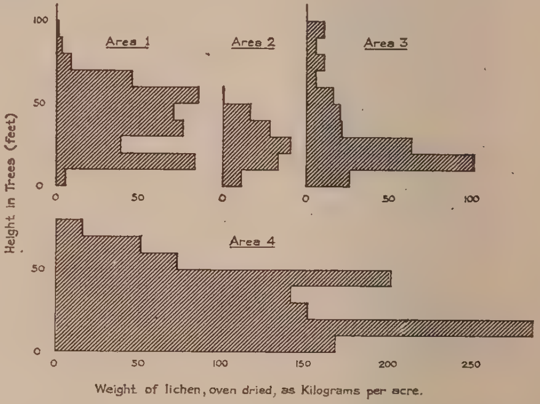

FIG. 1. Histogram showing the weights of Alectoria occurring in trees at successive ten foot intervals from the ground.

When snow melts in the spring, the ground beneath heavy lichen loads may be strewn abundantly with fallen lichens. Presumably frozen, brittle lichens are dislodged in quantity by winds, driven snows, and heavy loads of snow on the trees. The more exposed the lichens, the more vulnerable they are to such forces. This may partly explain the light loads in tree tops.

A characteristic feature of most graphs in Figures 1 and 2 is the relatively light lichen loads

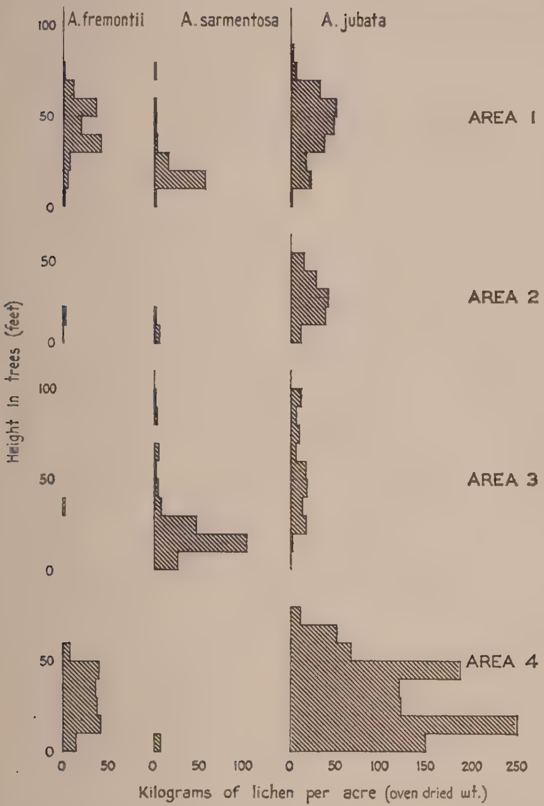

Fig. 2. Histogram showing the weights of three kinds of Alectoria in trees at successive ten foot intervals from the ground.

from 0-10 ft. These may be partly due to caribou and deer feeding upon lichen. Taylor (1922) reported that the scarcity of *Usnea barbata* near the ground may be caused by snow on the ground. He was unaware that he observed mainly Alectoria spp. not *Usnea barbata*. Depth of snow may influence the abundance of epidendric lichens in Wells Gray Park, but there is no simple relationship such as Taylor proposes. This is shown by abundant lichen near the ground at timberline, an area with deep snow in winter, and by the confinement of *A. sarmentosa* near the ground in several areas.

Perhaps the most important factors limiting the abundance of Alectoria are the shapes of trees, due in turn to the size of their branches. Short branches near the tops provide less space for lichens than do larger branches below, while a paucity of branches near the ground in closed stands could impose the same limitation. For example, data from Area 2 came predominantly from lodgepole pines. The shape of the figure for Area 2 in Figure 1 suggests the shape of a pine tree. Similarly, in Area 4 the spruce and fir tend to be conical in shape with longest branches low and near the ground.

Variations observed in the abundance of lichen through forest canopies will not be adequately explained until detailed studies evaluate the separate effects of many ecological influences.

Ecology of Alectoria

Smith (1921) states that the genus Alectoria inhabits the cool temperate zone. In British Columbia it grows in regions with relatively heavy precipitation, and may flourish in dry sites in the maritime climate near the Pacific Coast. Away from the sea dry sites in areas of heavy precipitation may contain Alectoria but its vigor may be low.

In his unpublished thesis, Szczawinski (1953) reported that in forests on the eastern slope of Vancouver Island, Alectoria spp. were most abundant and vigorous in most open and driest sites, while one species, *A. fremontii,* was confined to these sites. On better sites with less exposed location and more dense forests, Alectoria spp. were confined to tops of trees where exposure and other physical characteristics approximated those near the ground in poor, exposed sites. He stated also that "*Alectoria sarmentosa* and *A. jubata* are probably the most prominent heliophytes in corticulous sociations . . .," in the area studied.

In Wells Gray Park *Alectoria sarmentosa, A. fremontii,* and *A. jubata* differ in their occurrence with elevation. *A. sarmentosa* is common in lowland forests and on adjacent slopes to 5,000 ft, but is scarce at higher elevations. The other species do not appear to have this altitudinal restriction.

Figure 2 indicates that requirements of *A. sarmentosa* differ from those of the other two where all three occur in lowland forests. On all study areas, *A. sarmentosa* was mainly on branches of trees within 30 ft of the ground. In Areas 2 and 4, where this species was scarce, it was mainly within 10 ft of the ground. *A. sarmentosa* appears to favour the lower branches in dense forests as if requiring more sheltered sites where air movement and light intensity are reduced, temperatures are less extreme, humidity is increased, and mechanical injury from the elements is reduced. The separate effects of such a complex are difficult to unravel.

Alectoria jubata is not usually abundant at levels on trees where *A. sarmentosa* occurs (Fig. 2). Still, *A. jubata* appears to have wide ecological tolerance, occurring higher in the trees than other species in all areas. This ability to colonize the tree tops, together with relative abundance in the open, rather dry forest of Area 2, and impressive abundance in timberline forests, indicates a considerable tolerance to exposure. It is possible, however, that the apparent wide ecological tolerance of *A. jubata* is due to our considering it as one species, when in reality it may be a complex of several similar species.

A. fremontii is scarce or absent at levels where *A. sarmentosa* occurs (Fig. 2). Levels with relatively abundant *A. fremontii* are immediately above those with abundant *A. sarmentosa.* For example, in Area 3 *A. sarmentosa* abundance decreases sharply about 30 ft above the ground, while *A. fremontii* occurs only from 30 to 40 ft.

A. fremontii is not so successful in invading tree tops as is *A. jubata.* In all 4 study areas there were tree tops free of lichens, but there was much variation in the numbers of such trees, and in lengths of tops devoid of lichen (Table II). The exposed tree tops of a forest are in a drier climate than are more sheltered levels below. Presumably tree tops devoid of lichen are too dry to favour these plants. In Area 2 many tops of lodgepole pine had no lichen for comparatively long distances. This forest was relatively dry so the canopy was probably especially xeric. The absence of lichen in pine tops and the predominance of *A. jubata* below these tops supports *A. jubata* as probably the most xerophytic of the 3 lichens studied.

Contrasting with Area 2, most tree tops had lichen in Area 3, which probably has the most humid climate of the 4 study areas. The climate affecting Area 3 is illustrated by meteorological records from Blue River, B.C.; that for Areas 1 and 2 by data from Park Headquarters. Hythergraphs in Figure 3 illustrate the greater precipitation of the former. There are no meteorological data for Area 4, but from its location near timberline it is safe to say that temperatures are lower than in all other areas, and that precipitation is heavier than in Areas 1 and 2.

Lichens usually grow best in exposed places (Smith 1921), but the poor lichen growth found in Area 2, the pine forest, suggests the limitations of this requirement. These pines had the most open crowns of any trees sampled, yet Alectoria grew more luxuriantly in all other areas. An important factor here was probably moisture. Lodgepole pine forests are relatively xerophytic, while the other areas, especially 3 and 4, give floristic evidence of much higher humidity.

These ecological considerations have been mainly comparative among the species studied. Such terms as 'xeric' are relative, and here apply only to the region studied. Szczawinski (1953) found in the Douglas fir forests of Vancouver Island that Alectoria spp. were most successful in the driest forests, while their occurrence near the ground was confined to such forests. Since he was working in a region quite different in climate from that of Wells Gray Park, allowance must be made for these differences when comparing relative statements.

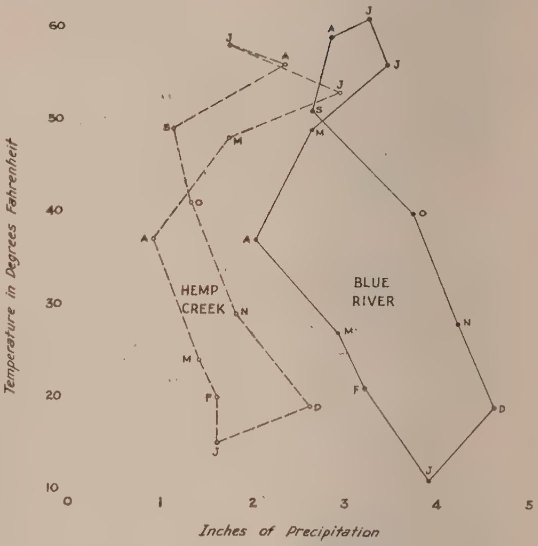

Fig. 3. Hythergraph for Blue River, near the eastern boundary of Wells Gray Park, and for Hemp Creek, in the southwest portion of the park.

Availability of Alectoria to Caribou

On standing trees.—Only lichens on lower branches of standing trees may be reached by caribou. The height that caribou can reach to gather food is thus of importance. In winter, when caribou feed heavily on lichen, the ground is covered with snow, variable in depth and ability to bear weight. Caribou may ordinarily be able to reach up to 8 ft from the ground while standing erect but snow may increase this distance. In Area 4, which in late winter may have snow depths of 7 ft or more with crust hard enough to support caribou, their effective reach may approach 15 ft. This maximum must vary, however, depending on snow depths and crust strengths. These are variables which complicate any measurement of lichen available to caribou. As Figure 1 shows, in all plots the amount of lichen growing from 10-20 ft is greater than that within 10 ft of the ground. In some plots the lichen load just above 10 ft is the heaviest on the trees, so the effect of snow on caribou reach above 10 ft is one of primary importance.

An additional variable affects the lichen within reach. In this study, distances from the ground for branches bearing lichen were measured from points of attachment of branches to trunks. Lower limbs of most conifers droops so that most foliage is 1-3 ft below the attachment point. Thus caribou with a reach of 8 ft can reach limbs attached approximately 10 ft from the ground.

Table II shows how height of reach would affect amounts of food available. With a reach of 10 ft, probably a generous allowance for caribou standing on bare ground, relatively small amounts of lichen are available. Reach to 15 ft would at least double the food available on all plots. In one plot this additional reach would increase the available lichen 9 times. A reach of 20 ft would increase available food 3 to 16 times, and make up to 42% of the total lichen load available. We believe that deep snow providing a firm footing for caribou is a variable determining the quality of this caribou range in winter. Successively higher reach as snows deepen enables caribou to obtain fresh supplies of lichen.

TABLE II. Treetops without Alectoria

Study area	No. trees examined	No. trees lichenless in top 5 feet	Average distance lichenless, in feet
1	11	6	8
2	13	8	25
3	12	0	—
4	11	3	5

On fallen trees.—Only a variable and frequently small fraction of lichen loads on standing trees is available to caribou; over half the load remains out of reach. Periodically, however, standing trees are felled by wind breakage and root decay. The full lichen load on the tree is then more or less available to caribou. Fallen trees are a major attraction to caribou, as noted in Ontario by Cringan (1956) and in the present study. Even near timberline where lichen loads near the ground on standing trees are particularly heavy, freshly fallen trees in winter may attract caribou, creating the greatest concentrations of feeding activity noted in our studies.

Cringan (1956) has postulated that in mature or other forests in which large trees are falling with some regularity, lichen carried to the ground may be an important source of food for caribou. He notes that enough falling trees could result in a sustained delivery of lichens to caribou from an abundant and growing supply held out of reach in trees, and so in no danger of being eaten in excess of growth increment. There is no doubt that this mechanism is in operation in Wells Gray Park. From timberline to lowest forests inhabited by caribou in winter, trees with their lichens fall every winter, many are found by caribou, and the lichen on them is eaten.

A major question is whether falling trees bring down enough lichen to make a major contribution to the supply of available food. It is possible to make some estimates of this contribution using weights of lichen obtained in this study.

In a forest typified by Area 3, there are 940 trees per acre with dbh of 2 in. or more. Table III shows the number of these trees by ages, their mortality and the lichen loads they carry. These figures are approximate, and indicate only roughly the amount of lichen that might fall with trees.

TABLE III. Theoretical Tree Mortality on Area 3, and Lichen Loads on Falling Trees, in 25 year period

Ages of Trees Years	No. Trees per acre	No. trees dying in 25 years	Lichen Load per tree (gms)	Lichen Load on Falling Trees through 25 years (Kilograms)
50- 75	450	200	50	10
76-100	250	90	100	9
101-125	160	110	700	77
126-150	50	35	1600	56
151-175	15	5	3100	155
176-200	10	5	4600	23
201-225	5	5	8600	43
Totals	940	450		373

The figures on tree mortality are obtained by subtracting the number of trees in one age group from the number in the previous age group. For example, the group of 450 trees 50-75 years old will lose 200 trees in 25 years, and there will then be 250 trees 75-100 years old. This calculation assumes there is no change in the structure of the forest with time, but trees are germinating, ageing, and dying, in such a manner that the age structure of the forest is more or less constant. This is an ideal concept, familiar as theory in forestry. Such a uniform age structure is found rarely in nature, although some uneven-aged forests approach this theoretical condition.

Table III shows that about 450 trees die in a 25 year period, or 18 trees die per acre per year. If the calculation went back to age zero, rather than age 50, the mortality figures would be much higher. Most mortality in trees takes place at an early age. Our data purposely excluded trees under 50 years old because they carried relatively unimportant quantities of lichen.

If the total load of lichen on trees falling over a 25 year period was 373 kg per acre (Table III), this represents an annual fall of lichen per acre of about 15 kg, oven dry weight. As seen in Table II, the lichen available per acre on standing trees in Area 3 is 26 kg below 10 ft and 56 kg below 15 ft. It appears that falling trees could be important in making additional lichen available to caribou, as Cringan's hypothesis suggests.

The importance to caribou of 33 lb of falling lichen per acre depends on whether other foods are plentiful or scarce at the time. If most trees fell in winter storms when snow was soft and food difficult to obtain, fallen trees with their lichen would be much more important to caribou survival than if most trees fell in the spring when melting snow was uncovering food on the ground. Limited field data suggest that most trees fall from January to April when food supplies may be critical. The importance of the lichens thus made available may be far greater than is suggested by the weight of caribou food involved.

On the ground.—When the snow melts in spring, in some forests of Wells Gray Park, considerable quantities of Alectoria appear on the ground. These have fallen from trees during the winter, and have accumulated at various depths in the deep snow. Data on the quantities of lichen involved suggest that amounts made available to caribou in this way may be considerable.

In the spring of 1959, lichens on the snow in 85 plots 1 m sq were collected, dried, and weighed. Plots were arbitrarily scattered through the forests inhabited by caribou in spring. Lichens collected were mainly Alectoria spp. but 28 samples contained small quantities of Cetraria sp. The weight of fallen lichen on each plot averaged 2.1 ± 1.9 g. This represents an occurrence of available tree lichens on the ground of 8.5 kg per acre. Over small areas this fallen lichen may exceed 50 kg per acre.

The extent to which caribou feed upon this temporary source of food is unknown, but fallen lichen could be important in spring. About half as much lichen falls free of trees in winter as is carried to the ground annually by falling trees. Like the lichens clinging to fallen trees, those on the ground are supplied by a sustained yield process from a source growing out of reach of caribou, and hence free of possible excessive use.

Discussion

An important condition uncovered by this study was the abundance of Alectoria on trees near timberline. Lichen loads of over a ton per acre, oven dry weight, constitute an unexpected abundance, even though casual observation had suggested that loads were heavy. This abundance and its concentration close enough to the ground to be available to caribou are probably major factors influencing caribou migrations in these mountains. As discussed by Edwards and Ritcey (1959), caribou inhabit forests near timberline from February to April when winter conditions are most severe, and when snow at this elevation may be 6-10 ft deep. One important condition enabling caribou to survive in these high elevation forests is that the deep snows are usually firm to walk on by February. The abundance of lichen must be an additional factor enabling caribou survival. Alectoria is abundant, a large percentage of the loads grow on branches near the ground, and deep firm snow increases the upward reach of caribou while feeding. A fortunate combination of environmental conditions appears to favor survival of caribou in winter in areas which seem anything but favorable at first glance.

Before February caribou are found in valley bottoms after descending from alpine meadows and timberline forests in October. In valley bottom forests (Area 3 is an example) they feed at first on herbs and evergreen shrubs. Later the snow is too deep for caribou to find these foods, and too soft for easy travel. The caribou then feed on Alectoria. The species of lichen available in greatest abundance on this early winter range is *A. sarmentosa,* a species scarce near timberline where *A. jubata* is the main form. Thus two species of Alectoria provide most food in winter, one in early winter, the other later.

Possibly caribou have no special preference for these lichens. In these forests in winter epidendric lichens are the only food available to caribou except for coniferous foliage which they apparently find unpalatable. Deep snow buries herbs and shrubs, so that conifers and the lichens on them are the only vegetable matter available to large herbivores.

Summary

Caribou in Wells Gray Park, British Columbia, appear dependent on epidendric lichens, Alectoria Ach., for food in winter. This study evaluated roughly the amounts of these lichens available to caribou. Lichen was collected from sample branches of trees in 4 study areas. It was oven dried, then weighed. From each sample the percentage composition by species was estimated.

Total lichen loads per acre ranged from 114-1332 kg. The latter value was from forest near timberline.

Vertical distribution of lichen loads varied among the areas. Loads were generally light within 10 ft of the ground, but were heavy immediately above this. Tops of trees had light loads, partly because branches were small, and partly because of exposure.

The 3 species of lichen, *Alectoria sarmentosa, A. fremontii* and *A. jubata* (the last may be a complex of similar species) showed quite different ecological tolerances. *A. sarmentosa* was confined to lower branches of forests at lower elevations. The *A. jubata* complex was most successful in all study areas and the most successful in exposed tree tops. The abundant lichen near timberline was mainly *A. jubata. A. fremontii* was less abundant than the other two species. In all study areas it was most abundant in branches immediately above those with abundant *A. sarmentosa.*

These lichens are available to caribou: on trees and within reach from the ground, on fallen trees, and on the ground after falling from trees.

Amounts of lichen on trees available to caribou vary according to several factors. Chief among these appears to be depth of snow. The deeper the snow the higher the reach of caribou into trees. If reach varies from 8-15 ft above bare ground, amounts of lichen available in areas studied ranged from 5-128 kg per acre.

A theoretical calculation of lichen available on falling trees, in a forest typified by Area 3, suggests that 15 kg per acre per year are available. Since most trees fall in severe winter weather, this source of food may be available when other food is scarce.

Fallen lichens accumulate in the snow through winter, and become available in quantity as the snow melts. Limited measurements suggest that about 8.5 kg per acre may be available on the ground in spring.

The great abundance of lichen on trees near timberline enable caribou to spend much of the winter in this zone of severe climate and deep snow. The settled snow of late winter enables them to reach higher into trees heavily laden with lichen. These high forests with severe winter climate are the most favored habitat in that season.

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SOME EFFECTS OF FIRE ON REPRODUCTION AND GROWTH OF VEGETATION IN NORTHEASTERN MINNESOTA

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INTRODUCTION

Fire as an important factor in determining the course of plant succession has been investigated by a number of workers. In the coniferous forests of the Lake States, however, insufficient emphasis has been placed on the detailed study of fire as an ecological factor. Maissurow (1941) maintained that for at least 5 centuries fire has been an important factor, burning 95% of the virgin forests of the area during this period. Chapman (1952) believed that most of the old, even-aged white pine stands throughout the Lake States area occur on burned-over land. A review of the published information on the ecological effects of fire will be presented elsewhere (Ahlgren and Ahlgren, in press).

This paper is an interim report on a long-range study of the effects of wild and prescribed fires in northeastern Minnesota. Material dealing with forest tree reproduction applicable to forest management was published separately (Ahlgren, 1959). The reproduction and growth of herbs, shrubs, and trees in relation to type and intensity of burning, soil conditions, and other environmental factors are considered here.

Because many burns were wild fires and therefore unpredicted, and because topography and plant distribution varied in the areas studied, it was difficult to obtain exact information concerning the condition of the land before the fires. However, comparisons were made with similar, nearby, unburned land.

The assistance and consultation of members of the U. S. Forest Service is gratefully acknowledged, as is the advice of Dr. E. V. Bakuzis and the assistance of the summer staff of the Quetico-Superior Wilderness Research Center.

METHODS

The field results are based largely on 11 series, each consisting of thirty 10 sq m circular plots placed 10 m apart. From these, quantitative data on tree reproduction and relative frequency of herbs and shrubs were obtained, all species listed, and the per cent of space occupied by each and height range recorded. The first, second, and third dominant herb, shrub, and tree species were also noted. Dominance rank was based on an estimate of relative abundance and per cent cover for the 3 major species. Age of all shrub and tree seedlings and sprouts was recorded from whorl or node counts. Ground line ring counts of nearby plants of the proper size were made when necessary.

More detailed observations of stages in the development of post-fire vegetation were obtained from 16 sites on one of the burned areas. On each site, 3 concentric plots, 1/1000, 1/50, and 1/10 acres were established. From the 1/1000 acre plots, exact counts were obtained of all herbs, shrubs, and trees, with height and per cent cover for each species. From the 1/50 acre plots, data were obtained on abundance, height, and per cent cover of all shrubs and trees less than 1 in. in diameter. Data on trees 1 in. in diameter and over were obtained from the 1/10 acre plots. On the 1/1000 and 1/50 acre plots, counts were made of both early and late summer vegetation. Tree data from the 1/10 acre plots were recorded annually. At each location, points were established from which early and late summer vegetation was photographed. These plots were placed in 14 locations throughout the burned-over area, and in 2 locations on comparable, unburned land.

Sprout or seed origin of post-fire plants was determined on transects 2 m wide and 20 m long placed at least 75 ft from the nearest study plots. All plants were carefully dug and examined to determine whether they were of seedling or sprout origin. Where mats or hummocks were involved, a representative sample was examined. Twelve such transects were established near Plot Series 1, 2, and 3, sampling both moist and well-drained sites. Two were placed near Plot Series 5 and 6.

Intensities of burn were recorded using the following terms: 1) a light burn is one in which surface fire consumed only loose litter, with slight scorching of crown foliage; 2) a hard burn is one in which surface fire consumed all litter and some duff, and tree crowns were killed by scorching; 3) a severe burn is one in which surface fire consumed all litter, duff, and some humus. Occasionally all humus was consumed, revealing mineral soil. The crown fire consumed all foliage and small branches up to 0.5 in. diameter.

Within each of the sixteen 1/10 acre plots, a soil pit was dug to bedrock or to a 5 ft depth and profile descriptions were made. Soil samples from representative profiles were analyzed for pH, available nitrogen, ammonia, calcium, phosphorus, and potassium by the University of Minnesota Soil Testing Laboratory. Moisture content and moisture holding capacity determinations were made, using methods described by Wilde and Voight (1955). Similar tests and descriptions were made on the 11 plot series.

Biological yield capacity of soil from the burned-over areas was obtained using samples from the upper 8 in. of soil from 5 burned-over areas and 5 comparable, unburned areas. Each soil sample was thoroughly mixed and placed in 4 one-gal., paraffin coated cardboard containers. Two containers of each sample were seeded with oats (*Avena sativa* L.) and two with sunflowers (*Helianthus anuus* L.), and were placed in a greenhouse. Distilled water was added when necessary. Plants were grown for 3.5 months. Weekly records were made of height, leaf width, color, and vigor. Every two weeks, samples of oats from each site were harvested, and fresh and dry weight determined.

STUDY AREAS

Approximately 1,000 acres in the Superior National Forest were studied. Land subjected to wild fire, prescribed burns, and corresponding unburned land were represented in the 11 series of plots. Information about these series is given in Tables I and II. Soils consisted of sandy loams merging with sand in the lower layers, in some cases underlain with clay. Charcoal was frequently found in the soil profiles, indicating the occurrence of past fires. Most of the areas had good drainage. In the depressions of Series 3, 5, and 6, supporting

TABLE I. Site history of the eleven series of 30 plots

Location	HEART LAKE				KEELEY CREEK			TOMAHAWK ROAD	PLUM LAKE		POLLY LAKE
Series no.	1	2	3	4	5	6	11	7	8	9	10
Fire history	800 acre hard to severe wildfire April 1952			unburned	40 acre severe wildfire July 1955		unburned	3, 20 acre units light prescribed burn May 1956			60 acre hard slash wildfire July 1952
Pre-fire forest condition	8 year jack pine plantation	jack pine with some black spruce	black spruce with some jack pine	jack pine with some black spruce and birch	jack pine-black spruce			clear-cut jack pine with some aspen and birch			
Organic layer, before fire after fire	2 to 6 in. 1 to 2 in.				2 to 6 in. 0 to 2 in.			2 to 6 in. 2 to 5 in.			2 to 6 in. 2 in.

TABLE II. Analysis of soils from series 1-11

Location		HEART LAKE				KEELEY CREEK			TOMAHAWK ROAD	PLUM LAKE		POLLY LAKE
Age of burn at time of soil analysis		5 years			unburned	2 years		unburned	4 months			6 years
Series		1	2	3	4	5	6	11	7	8	9	10
Soil depth at pit		2-3 ft.		1-2 ft.	over 5 ft.	3-4 ft.		over 5 ft.	4 ft.	over 5 ft.		4 ft.
Moisture holding* capacity		36.2	not tested		38.3	45.2	not tested	32.4	36.3	39.9	34.8	39.0
Moisture content (pct)*		24.5	"	"	22.0	33.7	" "	25.7	23.6	24.1	23.2	23.8
Organic matter (pct)	1-2 in.	8.5+			8.5+	5.9	8.5+	8.5+	8.5+	8.5+	8.5+	8.5+
	4-8 in.	2.8	"	"	1.8	2.1	1.6	6.6	3.9	6.2	2.8	3.0
	8+ in.	2.4			0.8	0.6	0.6	2.9	2.7	2.7	0.6	2.5
pH	1-2 in.	5.1			4.2	6.7	5.1	4.6	5.8	5.0	4.7	5.2
	4-8 in.	5.0	"	"	5.2	5.7	5.7	5.3	5.0	5.7	6.0	5.0
	8+ in.	5.4			5.5	5.6	6.3	6.2	5.4	6.6	6.2	5.3
Soluble salts (ppm)	1-2 in.	31.0			9.0	12.0	9.0	0	10.0	0	0	25.0
	4-8 in.	0	"	"	0	0	0	0	0	0	0	0
	8+ in.	0			0	0	0	0	0	0	0	0
Calcium (ppm)	1-2 in.	325.0			150.0	950.0	200.0	100.0	225.0	75.0	100.0	350.0
	4-8 in.	200.0	"	"	150.0	450.0	175.0	50.0	50.0	25.0	50.0	150.0
	8+ in.	275.0			125.0	150.0	200.0	150.0	50.0	175.0	tr.	125.0
Nitrate (ppm)	1-2 in.	65.0			70.0	65.0	65.0	tr.	tr.	tr.	50.0	75.0
	4-8 in.	75.0	"	"	75.0	70.0	65.0	60.0	50.0	tr.	tr.	80.0
	8+ in.	70.0			65.0	65.0	70.0	75.0	tr.	50.0	tr.	70.0
Ammonia (ppm)	1-2 in.	40.0			25.0	15.0	15.0	10.0	50.0	35.0	15.0	45.0
	4-8 in.	15.0	"	"	20.0	10.0	15.0	15.0	20.0	20.0	10.0	15.0
	8+ in.	15.0			15.0	15.0	10.0	10.0	20.0	15.0	15.0	15.0
Phosphate lbs./acre	1-2 in.	22.0			7.0	160.0	85.0	19.0	100.0	76.0	75.0	30.0
	4-8 in.	17.0	"	"	9.0	53.0	8.0	26.0	19.0	85.0	25.0	20.0
	8+ in.	16.0			8.0	5.0	9.0	10.0	10.0	10.0	30.0	16.0
Potash lbs./acre	1-2 in.	280.0			105.0	280.0+	230.0	110.0	175.0	225.0	210.0	280.0+
	4-8 in.	110.0	"	"	65.0	125.0	75.0	65.0	135.0	145.0	60.0	120.0
	8+ in.	85.0			60.0	40.0	50.0	35.0	50.0	85.0	30.0	75.0

*Average of 10 samples.

TABLE III. Site history for the 16 sets of 3 concentric plots

Plot	A	D	F	G	B	C	K	L	M	N	E	J	I	O	P	H
Pre-fire forest	jack pine				spruce-fir			8 year jack pine plantation	black spruce			aspen		tamarack bog	black spruce	jack pine
Burn intensity	hard	severe	hard	light	hard	severe	hard	hard	hard	severe	hard	hard		hard	unburned	
Post-fire organic layer	1 in.	2 in.	1 in.	2 in.	1 in.	2 in.	2 in.	1 in.	3 in.	6 in.	3 in.	1 in.	3 in.	3 in.	2 in.	2 in.

sphagnum and black spruce, however, the water table was within 2 ft of the surface and the site was moist.

A portion of the area in which Series 5 and 6 occur had burned over 3 years before. Noticeable erosion was observed in those parts of the reburned area where all organic matter had been consumed. Reburning apparently altered the soil mantle to such an extent that it was easily removed by rain and wind. This was the only place where extensive erosion was observed.

Series 7, 8, and 9 were submitted to prescribed burning, primarily to reduce fire hazard and improve the planting site. The areas had been logged and the slash placed in windrows 3 to 6 ft high. Less slash was present on Series 7 and was not completely piled. Surface fire between windrows was light on all 3 areas, but the litter irregularly and lightly burned. Under the windrows about 1 in. of litter burned, leaving up to 5 in. of unburned organic matter and ash on the ground. These areas were very similar to those of Series 1, 2, and 3, except that the topography of Series 7 was more rolling, creating a somewhat drier site, and the sandy loams of Series 8 and 9 were deeper.

Topography and soils of Series 10 were similar to those of Series 1, 2, and 3, but the area had been logged prior to burning, and green slash was scattered throughout. All surface litter and much duff were consumed, leaving a layer of ash and organic material 2 in. deep. The pre-fire condition of the organic layers was determined from unburned islands which occurred occasionally throughout the burned areas.

The 1/1000, 1/50, and 1/10 acre plots on which more detailed records were made sampled the natural variation within one area located near Series 1, 2, and 3. Description of these plots is given in Table III.

RESULTS AND DISCUSSION

Various factors are involved in the effect of wild and prescribed forest burning on plant succession. Such factors as pre-burn condition of the land, season of burn, seed supply, intensity, ash concentration, subsequent mineral nutrition, soil moisture, rainfall, humidity, soil and air temperature, animal populations, and plant competition all determine the response of vegetation.

Vegetational response has been divided into 2 aspects: 1) the frequency of occurrence of a given species, as determined by the ability of the plant to survive and reproduce following fire; 2) the subsequent dominance or importance and size of the plant as determined by its growth response to fire-caused changes in the environment, especially the soil.

Plant Frequency

In Table IV, plants have been grouped into 3 major classes: Class A, those which appeared only on unburned plot series; Class B, those which appeared only on burned-over series; and Class C, those which occurred on both burned and unburned series. This table gives information on the frequency of these plants in the series, their types of reproduction, and most frequent means of dissemination.

Class A, Species Found only on Unburned Series.—These species were minor associates in the vegetation, occurring sporadically on a small number of plots. All are perennials, reproducing mostly by shallow or surface rhizomes or bulbs, and are characteristically shade plants. Several factors may be related to their absence in burned-over areas. Their reproductive parts may be susceptible to heat damage or, as shade plants, they may have been unable to grow and compete with more light tolerant species in the openings created by fire. These species may reproduce by seed, but seedlings were infrequent. If seeds were present in the soil on the burned-over areas or dispersed into the areas after fire, apparently they were unable to grow and survive.

Class B, Species Found Only on Burned-over Series.—The majority of these species reproduced by seed. About one-third of these were wind disseminated and may have come into the area after fire. Seed of another third are reported to be dis-

TABLE IV. Frequency of species by series. Figures given in the table represent the percent of plots out of each thirty-plot series in which the species was found. The types of reproduction indicated are based on observations on twelve transects discussed in the text. *S* refers to seed origin, *V* to vegetative origin, *V-S* to vegetative and seed origin in about equal numbers. The small letter in parentheses indicates the less frequent method of reproduction. Information on 'Dispersal agent' is based on field observations and Martin, Zimm, & Nelson (1951)

Location	HEART LAKE				KEELEY CREEK			TOMAHAWK ROAD	PLUM LAKE		POLLY LAKE	Type of reproduction and dispersal agents
Burn intensity	Hard		Severe	Un-burned	Severe		Un-burned	Light			Hard	
Moisture	Well drained		Moist	Well drained	Moist		Well drained	Well drained			Variable	
Series	1	2	3	4	5	6	11	7	8	9	10	
Class-A Unburned Land Only												
Cypripedium acaule				10			13					
Cinna latifolia				3			7					
Goodyera repens				20			10					
Polypodium virginianum				7			13					
Class-B Burned Land Only												
Geranium Bicknellii	3	7	10		100	100		47	23		3	S—small mammals
Epilobium angustifolium	7	3	97		87	100		10	3		87	S—small mammals, wind
Epilobium glandulosum	3	3	7		60	93						S—small mammals, wind
Marchantia polymorpha					80	93				33	43	spore—wind
Corydalis sempervirens	3				50	43		17				S—gravity
Dryopteris spinulosa	3		33			3						V
Carex disperma	7	7	60									V (s)
Viola incognita	20		43									S (v)—song birds
Lonicera canadensis	7	7						13	40	47		V
Polygonum cilinode	73	80	97		83	57		47	3	7	30	S (v)—small mammals, song birds
Anaphalis margaritacea	7		13		17	7		7	7		33	S—gravity, wind
Aralia hispida	7	13	43		30	23		30	17	3	80	V-S—small mammals, song birds
Aster ciliolatus	27	7								10	53	V-S—small mammals, wind
Anemone quinquefolia	30	77	20		50	23		60	27	63		V-S—gravity
Comptonia peregrina	23	53	10		63	73						S—deer
Carex sp.	53	30	63		93	93		93	93	83	73	V (s)
Class-C Burned&UnburnedLand												
Cornus canadensis	100	90	97	90	87	67	93	97	100	100	90	V (s)—small mammals, song birds
Maianthemum canadense	40	100	40	93	70	47	90	87	100	100	40	V (s)—small mammals, grouse
Vaccinium angustifolium	93	100	97	97	63	63	93	87	73	97	90	V (s)—small mammals, birds, bear
Clintonia borealis	80	57	37	73	47	27	70	87	87	73	30	V (s)
Lycopodium obscurum	23	13	3	23		3	17	17	3	30	23	V
Aster macrophyllus	77	87	73	30	60	27	23	73	97	100	43	V (s)—small mammals, wind
Rubus idaeus	93	97	100	20	70	40	17	97	20	57	83	V-S—small mammals, birds, bear
Rubus pubescens	77	50	17	37	77	20	40	87	97	97	17	V-S—small mammals, birds, bear
Viola spp.	7			7	3	3	3	37	23	47	73	S (v)—small mammals, song birds
Alnus crispa	50	37	43	23		3	17	83	83	17	63	V
Ribes glandulosum	20	7	30	7		3	3	17			63	S—small mammals, song birds
Pinus Banksiana	33	90	50	37*	97	93	40*	40	7	23	93	S—wind
Betula papyrifera	13	20	97	20*	83	100	13*	73	93	80	17	V-S—wind
Fragaria vesca	33	30	10	3	3	3		10		7	13	V-S—small mammals, song birds, grouse
Pyrus americana	27	17	20	67		7	73	40	3	13		V-S—song birds, grouse
Aralia nudicaulis	47	57	40	67	40	30	63	87	90	73	17	V (s)
Gaultheria hispidula	3		67	20			17		13	7		V-S—small mammals
Populus tremuloides	23	7	30	10	77	80	10	33	3	17	70	V-S—wind
Dryopteris Thelypteris	3		33	7	17	20	10	13	10		3	V
Picea mariana	3	17	93	77	87	97	67		17	10	50	S—wind
Apocynum androsaemifolium	37	63		13	13		7	3	43	67	3	V-S—wind
Linnaea borealis	47	77	33	13	43	17	17	57	67	70		V
Oryzopsis asperifolia	77	100	10	33	50	20	37	80	47	87	33	V-S—gravity
Amelanchier sp.	60	73	13	33	10	13	30	27	50	67	23	V
Corylus cornuta	83	37	3	70	17		73	43	93	80	3	V (s)—small mammals
Diervilla Lonicera	100	93	33	50	30	30	53	93	100	97	87	V (s)
Trientalis borealis	10		3	7		3	7	13	33	40	13	V-S
Rosa acicularis	40	50	43	50	50	10	57	60	87	83	13	V (s)—small ammmals, song birds, grouse
Calamagrostis canadensis	93	100	67	33	83	37	30	83	30	23	67	V (s)—wind

* Mature trees included.

seminated by birds and small mammals (Martin et al. 1951, Krefting and Roe 1949). Of the remainder, half produced seed which merely dropped to the ground and half are species disseminated by larger animals such as deer and bear. Some of these seed could have survived fire in the lower layers of soil and could have been stimulated to germination by heat, as reported for several species (Stone and Juhren 1951, Wright 1931, Ahlgren 1959).

Variations in fire severity affected species distribution in several ways. The thick ash layer on the soil surface in severely burned areas resulted in high concentrations of potassium, nitrogen, ammonia, and calcium, while on the lightly burned areas, ash additions were not great (Table I and II). Various species require different concentrations of minerals for optimum germination and growth. Heikinheimo (1915) reported that germination of some tree species, especially spruce and birch, is inhibited by ash. The higher temperatures on the severe burns undoubtedly killed underground parts of vegetatively reproduced species, thus eliminating them from competition. *Lonicera canadensis* Bartr. was frequent only on lightly burned plot series (8 and 9) where its underground parts survived and sprouted vigorously. *Polygonum cilinode* Michx., a species reproduced by seed, was absent on these lightly burned series and abundant on severely burned series. This species may require open conditions and may not be able to compete with sprouting species on light burns. However, it is also possible that either the ash content of the soil or the heat of fire may have stimulated germination.

On those series with higher moisture levels (3, 5, and 6), plants reproducing by seed or spores occurred frequently, comprising a major portion of the early post-fire vegetation. The severe fires on these sites reduced the organic layer to a moist, firm seedbed conducive to seed germination, in contrast to the thicker layers on light burns which formed a dry, hot surface in which young seedlings could not survive. Two vegetively reproduced species, *Dryopteris spinulosa* (O. F. Muell.) Watt and *Carex disperma* Dew. occurred in higher numbers on one moist series (S. 3). This series, however, included patches of unburned sphagum in which vegetative parts of these species survived the fire.

It is recognized that some species distribution differences are the result of chance. However, some examples of possible site specificity may be cited: *Anaphalis margaritacea* (L.) C. B. Clarke, *Aralia hispida* Vent., and *Aster ciliolatus* Lindl., which occurred on Series 10 more frequently than elsewhere, and *Anemone quinquefolia* L., which was absent on Series 10 and frequent on the other burned series. *Comptonia peregrina* (L.) Coult. was found primarily on Series 2, 5, and 6 which had not been logged before the fires and on which many burned tree trunks remained erect. Martin et al. (1951) reported that *Comptonia* is used as food by deer and grouse. These animals may have spread the species into the area. Both were noted there and may prefer land in this condition over lands clear cut before burning. *Carex spp.*, *Prunus pensylvanica* L., and *Salix* spp. were fairly frequent on all burned series, but were absent on the unburned series. *Pteridium aquilinum* (L.) Kuhn and *Oryzopsis pungens* (Torr.) Hitchc. were abundant in localized, well-drained burned areas.

The following species were also found only on burned-over areas, but in numbers too small to indicate possible site selectivity, although many are characteristic fire followers:

Acer rubrum L.
Acer spicatum Lam.
Actea rubra (Ait.) Willd.
Agropyron repens (L.) Beauv.
Agrostis alba L.
Agrostis scabra Willd.
Antennaria munda Fern.
Arctostaphylos uva-ursi (L.) Spreng.
Aster umbellatus Mill.
Athyrium Filix-femina (L.) Roth.
Brassica nigra L.
Cardamine parviflora L. *var. arenicola* (Britt.) O. S. Schulz
Chenopodium album L.
Chimaphila umbellata (L.) Bart. Scop.
Cirsium arvense (L.) Scop.
Clematis verticillaris D.C.
Cornus rugosa Lam.
Danthonia spicata (L.) Beauv.
Dragocephalon parviflorum Nutt.
Epilobium palustre L.
Festuca saximontana Rydb.
Gaultheria procumbens L.
Geum pratense Jacq.
Glyceria canadensis (Michx.) Trin.
Hieracium canadense Michx.
Juncus tenuis Willd.
Lactuca canadensis L.
Lathyrus ochroleucus Hook.
Lonicera dioica L.
Lonicera hirsuta Eat.
Lycopus americanus Muhl.
Panicum lanuginosum Ell.
Phalaris arundinacea L.
Phleum pratense L.
Poa palustris L.
Potentilla norvegica L.
Prunella vulgaris L.
Ribes hirtellum Michx.
Rubus spp.
Rumex Acetosella L.
Solidago spp.
Sonchus arvensis L.

Stellaria spp.
Streptopus roseus Michx.
Symphoricarpos albus (L.) Blake
Trifolium repens L.
Vaccinium oxycoccus L.
Vicia americana Muhl.

Class C, Species Occurring on both Burned and Unburned Areas.—This class differs from Class B primarily in containing a number of vegetatively reproduced species which survived the fire. Species in this category show different effects with different intensities of burning, as do plants in Class B. Vegetative parts of several species were remarkably fire tolerant and were equally distributed on unburned, lightly burned, and severely burned areas (e.g. *Cornus canadensis* L., *Maianthemum canadense* Desf., *Vaccinium angustifolium* Ait., *Clintonia borealis* (Ait.)Raf. In addition, *Calamagrostis canadensis* (Michx.)Nutt. also occurred irrespective of fire severity and was reduced only on series where vigorous shrub species competed. *Aralia nudicaulis* L., *Rosa acicularis* Lindl., and *Trientalis borealis* Raf. were less fire tolerant and were relatively infrequent on all burned areas except those which were only lightly burned. *Ledum groenlandicum* Oeder was less frequent on burned-over series, except for Series 3 where *Ledum* was a major shrub prior to fire.

Many species show a distribution influenced by their natural preference for moist or well-drained sites, but the combination of moisture and firm seedbed made the moist sites adapted to the establishment of a large number of seed-reproduced species, many not necessarily associated with moist sites. Seedlings of *Gaultheria hispidula* (L.) Bigel., *Ribes glandulosa* Grauer., *Viola* spp., *Populus tremuloides* Michx., *Picea mariana* L., *Rubus idaeus* L., *Betula papyrifera* Marsh., and *Fragaria vesca* L. were more frequent here.

Light may also have been a factor in the distribution of species reproduced by seed. Many were species which normally occurred on sites with high light intensity and consequently were not in the forest stand before the fire. They were also infrequent on those burned-over areas where a dense stratum of vegetative sprouting herbs and shrubs came in first and shaded the ground.

High soil moisture content may be involved in the destruction of underground parts of some vegetatively reproduced species. Several otherwise vigorous species were notably less frequent on moist, burned-over sites after fire (*Apocynum androsaemifolium* L., *Corylus cornuta* Marsh., *Diervilla Lonicera* Mill., *Linnaea borealis* L., *Oryzopsis asperifolia* Michx., *Amelanchier* spp.). Uggla (1958) showed that soil moisture tends to condense in the upper soil stratum and to function during fire as a thermo-insulator, protecting lower levels from high temperatures. This moisture, however, in the uppermost layer of organic soil, forms steam during intense fires. Such moist heat is more damaging to living tissue than the dry heat to which vegetative parts would be subjected on drier sites.

On the other hand, there are several species which reproduce largely by vegetative means, and which occurred on both burned-over and unburned lands, or were present in larger numbers on severely burned land: *Carex* spp., *Clintonia borealis* (Ait.) Raf., *Cornus canadensis* L., *Lycopodium obscurum* L., *Maianthemum canadense* Desf., *Aster macrophyllus* L., *Vaccinium angustifolium* Ait., *Rubus idaeus L.*, *Rubus pubescens* Raf., and *Alnus crispa* (Ait.) Pursh. Vegetative parts of these species must be very resistant to heat damage.

In general, then, it appears that the occurrence of vegetatively reproduced species on these burned-over lands depends primarily on the resistance of the reproductive parts to fire or their escape from it.

Much seed from scorched jack pine crowns germinated. Five to 7 yr. later, the resultant seedlings began to produce cones. Eighty per cent of the seed from these young post-fire trees was viable, and it became a factor in re-establishing jack pine in these areas. Cone production was earlier and more abundant than cone production on nearby plantations containing jack pine of the same ages.

There are interesting differences within genera in relation to distribution after fire. For example, *Aster macrophyllus* belongs in Class C and is frequent throughout the area irrespective of fire, while *A. ciliolatus* is limited to dry, burned-over series. Similarly, *Oryzopsis asperifolia* was frequent on all series, while *O. pungens* occurred only on dry, burned-over series. *Aralia nudicaulis* appeared on all burned and unburned plot series, while *A. hispida* was only on burned-over series.

The following plants occurred on both burned and unburned series in numbers too small to reveal differences in optimum site conditions: *Equisetum sylvaticum* L., *Galium triflorum* Michx., *Pyrola,* spp., *Abies balsamea* (L.) Mill., *Schizachne purpurascens* (Torr.) Swallen., and *Cornus stolonifera* Michx., *var. Baileyi* (Coult. & Evans) Drescher.

Reproductive Methods and Distribution

Seed and vegetively reproduced species were affected differently by different degrees of burn severity. Table V shows the per cent of vegetative and seed reproduction on burned-over land for Class B and Class C species during the first and subsequent growing seasons. The majority of species of both classes appeared the first growing season following fire. As mentioned before, vegetative reproduction, more frequent among Class C species, occurred most abundantly on lightly burned areas where there was little destruction of underground parts and sprouting covered the area rapidly. On the other hand, seedlings, more frequent among Class B species, were mostly on severely burned, moist areas where vegetative sprouting did not compete and seedbed conditions were favorable.

TABLE V. Types of reproduction associated with Class B and Class C species distribution. Figures given are taken from burned areas only and are based on 100% vegetative and seed reproduction during the 5 year period. This table includes those species listed in Table IV and those given in the text as occurring in infrequent numbers. Those species reproduced on the burn both vegetatively and by seed are included under both headings in this table

	Initial Appearance (year)	Vegetative Reproduction (%)	SEED REPRODUCTION			Total Reproduction (%)
			From Fleshy Fruit (%)	From Dry Fruit (%)	Wind Borne Seed (%)	
Class-B Species	1	25	6	23	11	65
	2-5	9	7	10	9	35
Total......		34	13	33	20	100
Class-C Species	1	46	18	5	14	83
	2-5	12	2	3	0	17
Total......		58	20	8	14	100

Wind disseminated seed occurred in both Class B and Class C. This agrees with Lutz (1956) who found wind dissemination to be important in the establishment of post-fire vegetation. However, as seen in Table V, other types of dissemination must also be considered. Species producing dry fruit with hard seeds occurred more frequently in Class B, found only on burned series, while fleshy-fruited species are more significant in Class C, found on both burned and unburned series. These results agree with reports by Kujala (1926) and Petterson (1931) that shrubs with fleshy fruits regenerate slowly after fire. Several factors may be involved in the difference in distribution. On severely burned series on which many Class B species were found, pre-burn vegetation may not have included as many fleshy-fruited species, hence fewer seeds of these were in the soil before the fire. Or, seeds from fleshy fruits are less heat resistant and therefore come in most frequently on lightly burned, well-drained sites where their seeds would be damaged less by fire. Post-fire dispersal by animals and birds must also be a factor. Conditions immediately following fire on lightly burned or unburned areas may be more conducive to bird and animal activity than conditions on severely burned areas.

Dominance and Growth

Figure 1 represents the extent of dominance of various species on each series. One of the major factors in the pattern of growth and dominance of the various species is the type of reproduction most common for it. Where vegetatively reproduced species survived and sprouted, they usually competed successfully against seed-reproduced species. On the other hand, where fires were severe and killed vegetative parts, seed-reproduced species obtained a rapid, often temporary dominance. This confirms findings of Ludi (1945) who believed that the major post-fire species are those present on the area before fire. Examples of this may be noted in *Aster macrophyllus* and *Diervilla Lonicera*. These species were less frequently dominant on moist than on dry series even though reference to Table IV reveals that they were present in all areas. These plants reproduced mostly by sprouting. On dry sites, vegetative parts survived, sprouted rapidly, and the species became dominant. On moist sites, vegetative parts were destroyed, reproduction was by seed, the response therefore delayed, and the species did not obtain a dominant position. *Rubus idaeus* and *Calamagrostis canadensis* are also more frequently dominant on burned areas, with a reduction in dominance on the moist sites less obvious.

Dominance of *Cornus canadensis, Vaccinium angustifolium, Rosa acicularis, Oryzopsis asperifolia, Corylus cornuta,* and *Alnus crispa* was similar for burned and unburned areas. All reproduced by sprouting. Those variations in dominance which did appear were probably due to natural, pre-fire distribution. Flowering and fruiting of some, however, especially Vaccinium, was favored on burned-over land. *Maianthemum canadense, Clintonia borealis, Lycopodium obscurum,* and *Linnaea borealis* were less frequently dominant on burned-over than on unburned series. These species reproduced by shallow, underground parts which may have been killed by fire. While Clintonia was abundant on burned Series 8, this area was only lightly burned, and damage to upper soil layers was not great. *Epilobium angustifolium, Geranium Bicknellii, Ribes glandulosum,* and *Polygonum*

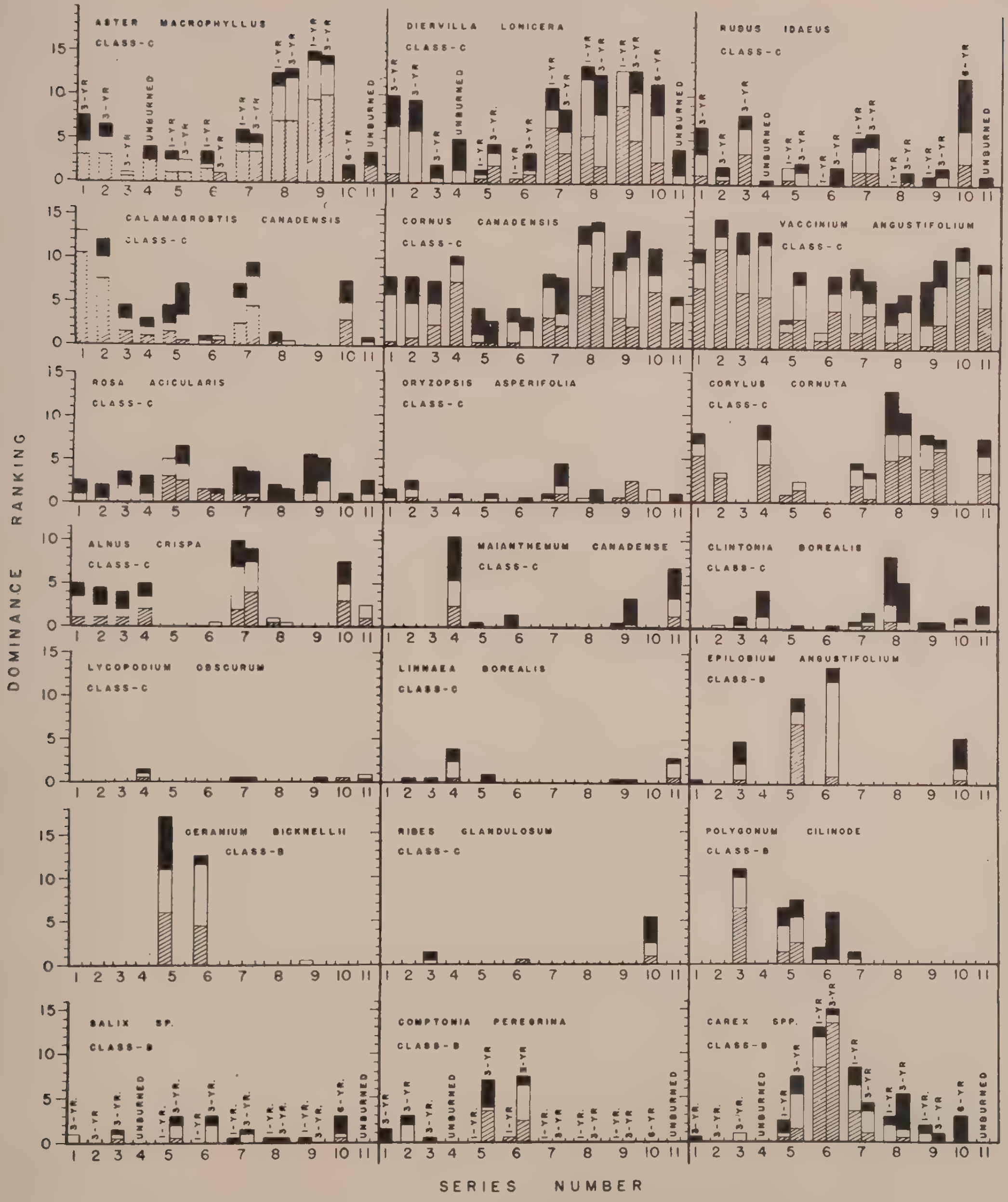

FIG. 1. Graph showing extent of dominance of various species on burned and unburned Series 1 through 11. The lined portion of each bar indicates the number of plots out of thirty in which the species was first dominant, the clear portion indicates the number in which it was second dominant, and the solid section indicates the number in which it was third dominant. For Series 5 through 9, two bars are given representing the first and third growing seasons following fire. For all others, only one observation is given, the year as indicated.

cilinode are dominant only on burned areas. All reproduced by seed and were more important on moist, severely burned sites.

For Series 5 through 9, species dominance for the first and third post-fire growing seasons have been presented in separate bars in Figure 1. Examination of these reveals certain herbs (*Carex* spp., *Polygonum cilinode, Epilobium angustifolium*) and some woody plants (*Comptonia peregrina, Salix* sp., *Diervilla Lonicera, Vaccinium* *angustifolium*) generally increased on Series 5 and 6. Decreases on these moist series can be noted for *Geranium Bicknellii, Aster macrophyllus* and *Cornus canadensis*. The reverse response frequently can be noted for these species on drier series (7, 8, & 9). Certain species just began to occupy a position of dominance on some sites 5 yr. after burning (*Corylus cornuta* Series 5, *Rubus idaeus* and *Ribes glandulosum* Series 6).

Five-Year Changes in Vegetation Cover

Figure 2 gives the changes in per cent cover for 5 yr. for the major species on each of the 1/1000 acre plots described in Table III. A rapid increase in vegetation began the first 2 yr. following fire on all burned-over plots. In most cases, this increase continued, but changes occurred in relative importance of various species.

Grass (*Calamagrostis canadensis*) dominated plots A, B, and C from the first year (see also Figure 3, nos. 1 and 2). All other species (e.g. *Cornus canadensis, Maianthemum canadense, Clintonia borealis*) declined as grass increased. In plot D, however, (see also Figure 3, nos. 5 & 6), *Aster macrophyllus* continued a rapid increase after the third year, while grass began to decline. Plots E, F, G, and K show rapid increase of *Cornus canadensis* in mixed vegetation. This increase also occurred under *Aster* cover in Plot D and under heavy shrub cover in Plots I and J (see Figure 3, nos. 3 & 4 and 5 & 6).

The majority of species which came in vigorously the first 2 yr. and maintained an important position during the 5 yr. period were of vegetative origin. Plants reproduced by seed (*Rubus idaeus* Plots C and E, *Polygonum cilinode,* Plots K and M, *Ribes glandulosum,* Plot K) were temporary and frequently began to decline the third or fourth year. Some of the vegetatively reproduced species, especially *Vaccinium angustifolium* and *Ledum groenlandicum* reached a position of dominance more slowly.

In none of the graphs is there any evidence of a stable condition having been reached at the end of 5 yr. This, together with the shifts in dominance noted in Figure 1 for Series 5 through 9, reveals that the vegetation is still in the process of active change and gives indications of the rate of succession.

Tree reproduction became established within the cool, moist microenvironment created by the lush, herbaceous cover. These conditions are optimum for early tree seedling growth. Trees began to gain in per cent cover after 3 growing seasons, (Plots D and G *Betula papyrifera,* Plots F and N *Pinus banksiana,* Plot I *Populus tremuloides*). Although sprouting might be expected to be more rapid than seedling growth, this delayed response of trees occurred among those species reproduced by sprouts as well as those reproduced by seed. Delayed response of sprouts was also found in shrubs growing on severely burned plots (*Ledum groenlandicum* Plots E and M, *Vaccinium angustifolium* Plots E, N, and M, and *Corylus cornuta* Plot F). Heat damage to underground parts may have been a factor in the delay.

No stimulation of growth was observed on the unburned series. On unburned Plot H, for example, (Figure 3, nos. 7 & 8, and Figure 2) with a mature jack pine crown closure of 65%, there were only slight fluctuations in per cent cover of *Cornus* and *Maianthemum*. On unburned Plot P, where wind damage caused the mature black spruce stand to begin to break up during the third year of observation (Fig. 2), there was a gradual increase in *Vaccinium,* possibly correlated with increased light and temperature.

Responses to Differences in Soil Nutrients

It is apparent that fires have influenced distribution, reproduction, and growth of various plant species. Several factors, such as light, moisture, temperature, and soil nutrients are involved in development of vegetation. Fire may cause significant changes in all these factors. However, in this study it was not possible to follow light and temperature changes. Tables I and II give the range of differences in other conditions on burned and unburned study areas. It can be noted that upper layers of soil in all burned-over areas contain more phosphate, potash, soluble salts, and calcium than comparable, unburned study areas. This increase is undoubtedly caused by release of nutrients from ash (Fowells and Stephenson 1933 and Garren 1943).

In a previously published report, the author has shown (Ahlgren 1959) that, while soil nutrient concentrations were highest immediately after fire, they remained high for up to 5 years. The rate of leaching varied for different nutrients. The additional nitrate contributed by ash apparently diminished rapidly. There are reports of both loss (Lutz 1956, Barnette and Hester 1930) and increase (Heyward and Barnette 1934, Garren 1943, Lunt 1951) in nitrogen in soil after burning. These conflicting results may be due to different rates of leaching on different soils. On the soils involved in this study, content of potash and phosphate diminished more slowly than did nitrate. Five or 6 yr. after fire, soil content of these nutrients was still higher than on comparable, unburned land.

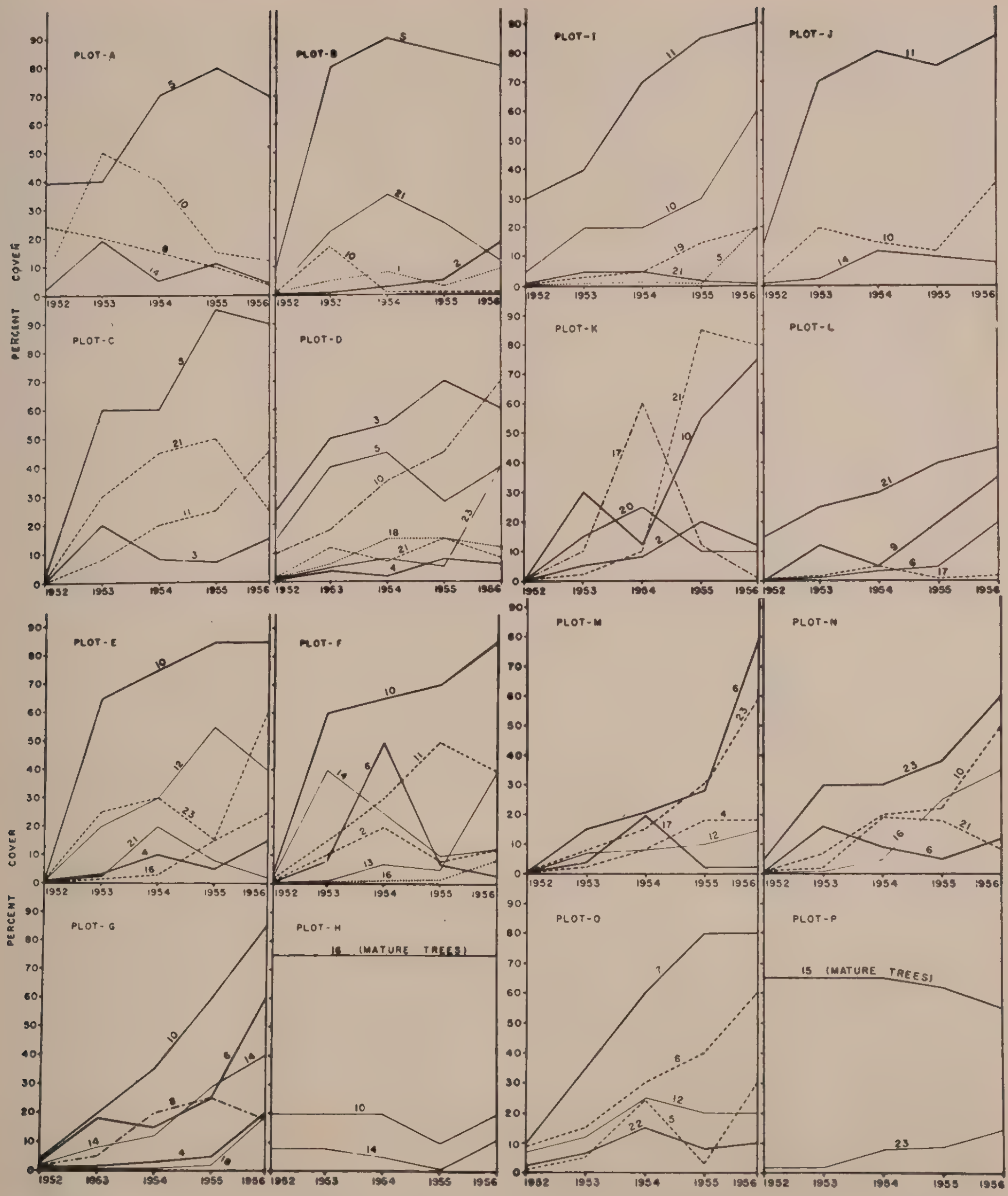

Fig. 2. Graph giving the per cent cover for 5 yr. on the 1/1000 acre plots. The number given above the plotted lines refers to the individual species given on that line: 1. Amelanchier sp.; 2. Aralia nudicalis; 3. Aster macrophyllus; 4. Betula papyrifera; 5. Calamagrostis canadensis; 6. Carex spp.; 7. Chamaedaphne calyculata; 8. Clintonia borealis; 9. Comptonia peregrina; 10. Cornus canadensis; 11. Corylus cornuta; 12. Ledum groenlandicum; 13. Linnaea borealis; 14. Maianthemum canadense; 15. Picea mariana; 16. Pinus banksiana; 17. Polygonum cilinode; 18. Prunus pensylvanica; 19. Populus tremuloides; 20. Ribes glandulosum; 21. Rubus idaeus; 22. Salix sp.; 23. Vaccinium angustifolium.

Field observations in burned areas revealed a rapid growth rate and marked lushness in size, color, and leaf thickness for many species the first few post-fire growing seasons. While increased light created by destruction of overstory may have contributed to this, the fertilizing action of nutrients from the ash was more directly involved. This growth stimulus was especially evident the first growing season when nitrates, as well as other nutrients, were at high levels. The stimulation

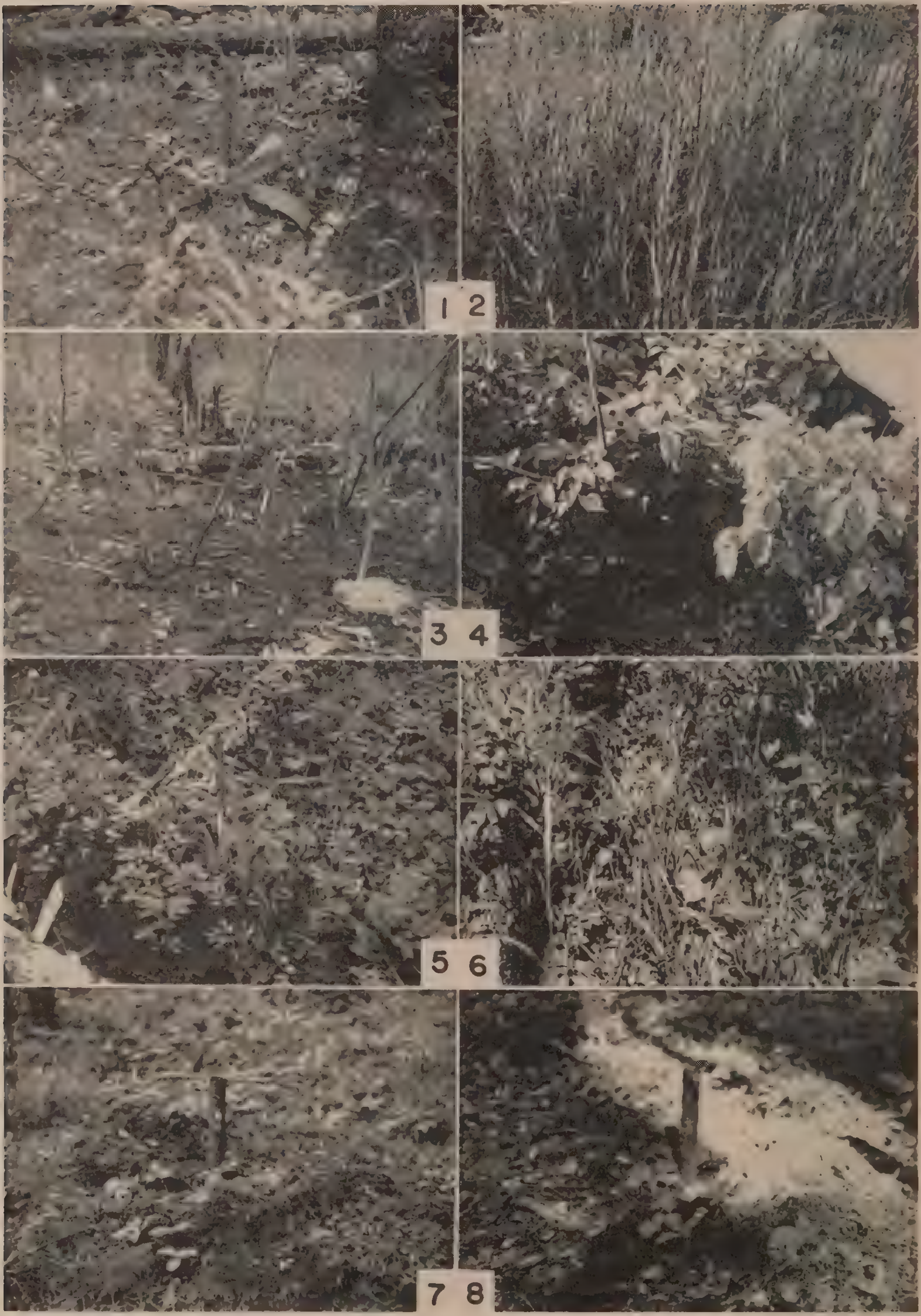

FIG. 3. Numbers 1, 3 & 5 illustrate the development of vegetation on various plots 3 months after fire. Numbers 2, 4, & 6, respectively, are the same plots 5 yr. later. Numbers 7 & 8 are an unburned plot at the same time interval.

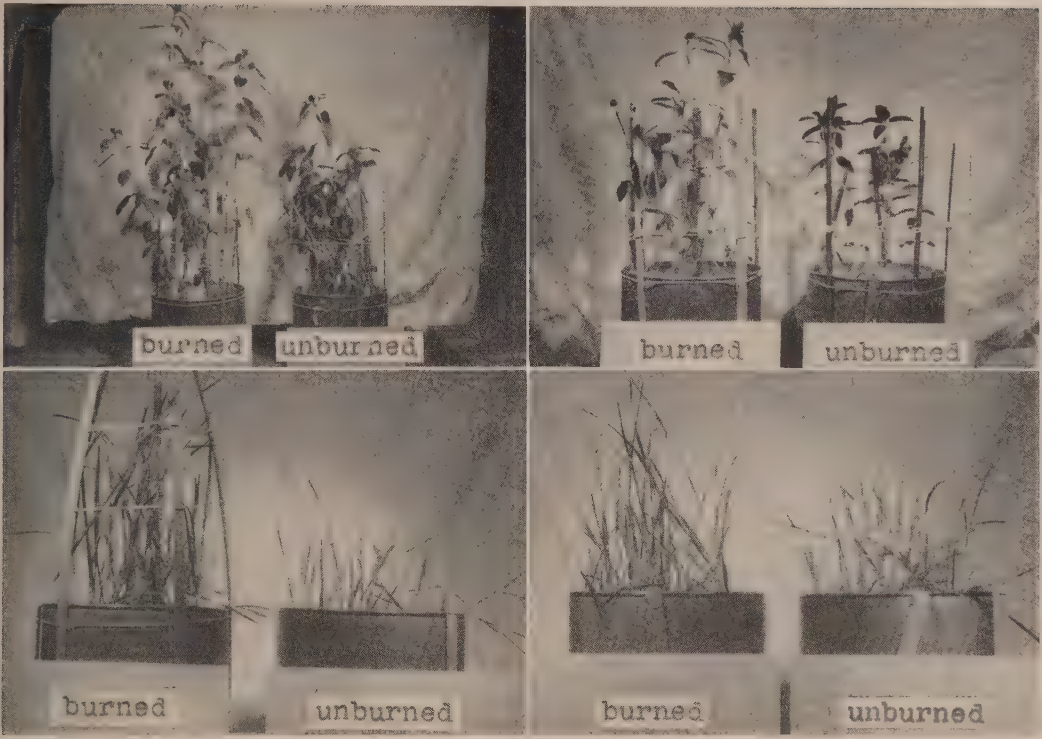

FIG. 4. Oats and sunflower grown on soil from burned and unburned areas. The two pictures on the left are of plants grown on soil from an area burned 4 months previously. The 2 pictures on the right are of plants grown on soil from an area burned 5 years previously.

continued, although not as marked, for several years, corresponding with soil analysis which showed ash nutrients to be leached out slowly.

To obtain some indication of the effect of nutritional differences on plant growth, sunflower and oats were grown on soil from Series 2, 5, and 8, and from 2 newly burned-over areas not described in this study. As shown in Table VI, the plants grown on soil from burned-over areas were heavier than those grown on soil from comparable, unburned areas. This difference is also seen in Figure 4. Plants on soil from burned-over areas had wider leaves, darker color, and fewer necrotic patches and less withering of leaf tips. Plants on soil from Series 5, however, showed no increase in size. Table I indicates this series was subjected to a severe summer fire which resulted in a large amount of ash on the soil surface and a corresponding increase in nutrients. It is possible that in this case the addition of ash was great enough to inhibit plant growth, since growth of oats is inhibited when greater than normal amounts of certain nutrients are in the soil (Lyon et al. 1952). Large additions of ash were also present in one of the newly burned-over areas. In this case, plants on soil from both the burned-over and unburned areas grew well, indicating a high degree of soil fertility even prior to fire. This generally good soil fertility, together with high concentration of nitrogen on the burned-over series, may have overcome the inhibition caused by the excess of certain nutrients. Stimulation and inhibition of plant growth on burned-over land is difficult to relate to specific mineral deficiencies or excesses. Some workers have tried to circumvent this by postulating the heat-induced formation of inhibiting or stimulating substances in the soil, independent of ash concentrations (Seaver and Clark 1912, Pickering 1910).

Evidence of the influence of soil mineral concentration on water absorption is found in the difference in per cent water content among plants on various soil samples (column 3, Table VI). In most cases, plants grown on soil from burned-over areas contained one to 2½% more water than those from unburned areas. Exceptions were soil from one of the newly burned-over areas and from the 3 year old burn (Series 5), where plants on soil from the unburned area contained 1% more water. Both these areas had surface ash content higher than that of other samples tested. This may have contributed to the reduction in water

TABLE VI. Biological yield capacity of soils from areas burned at different times, compared with soil from comparable, unburned areas. Results are expressed as per cent increase in yield, burned over unburned sites, of oats and sunflower grown in samples of these soils under greenhouse conditions

Time Since Burned	Increase in Fresh Weight Burned over Unburned (%)	Increase in Dry Weight Burned over Unburned (%)	Increase in Water Content Burned over Unburned (%)
4 months..	18	21	−1.0
4 months...	35	24	2.4
2 years....	38	28	2.0
3 years....	−10	7	−1.0
5 years....	65	63	1.0

content through a change in osmotic balance between roots and soil.

CONCLUSION

As a result of the interplay of factors discussed, the burned-over land was rapidly covered the first and second growing seasons with lush vegetation, predominately herbs. Depending on fire severity, this was about equally of seed and vegetative origin. This lush first and second year growth was important in determining subsequent plant succession. It created a shady, moist, cool microenvironment on the soil surface, conducive to the early growth of woody plants, especially tree species. It also trapped and retained nutrients released to the soil by ash, reduced leaching, and began the rebuilding of the damaged organic layer. In addition, it provided food and satisfactory cover for animal life, especially certain small mammals and birds.

These early plant invaders retained a position of dominance for several years. However, after the third growing season, woody species began to dominate and will undoubtedly be important in the future vegetation. Similarly, future changes in mineral content of soil and wild life populations will undoubtedly be found.

SUMMARY

Plant succession on land burned by wild fire and prescribed burning has been followed and compared with plant succession on unburned land. The herbs and shrubs on the study areas were divided into 3 major groups: 1) those only on unburned land; 2) those appearing only on burned-over land; and 3) those which were on both burned-over and unburned land. Species in the first group were minor associates, occurring sporadically in the area. The few species included in the group were all vegetatively-reproduced perennials, and were characteristically shade plants. They did not appear after fire, either because their reproductive parts were destroyed, or because they were unable to grow and compete with more light tolerant species in the opening created by the fire.

The second, larger group consisted mostly of seed-reproduced annuals plus a few vegetatively-reproduced species which were undoubtedly in the area before fire. Included in this group are well-known fire followers. Seed reproduction was prominent on moist, severely burned sites where underground parts of vegetatively-reproduced species would have been killed by fire, and moist conditions would favor seed germination. Many of these species were primarily wind disseminated and could have blown into the area after fire. Others were disseminated by animals, primarily birds and small mammals. These could have been disseminated after fire, but it is probable that many were in the soil before the fire and were not destroyed by it.

The third group consisted of both seed- and vegetatively reproduced species which comprise the characteristic ground cover of the area. These showed not only a tolerance for fire, since underground parts of many survived it, but also a tolerance for shade, since many were major components of the forested, unburned land.

The added nutrients from the ash contributed to a lush growth of early post-fire vegetation. This vegetation not only utilized and retained minerals from the ash which might otherwise have been lost by leaching, but also provided the cool, moist microenvironment necessary for young tree seedling growth. Much of this vegetation was temporary, and began to decrease in dominance when the tree seedlings became more light tolerant and began to assume the dominant position.

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THE MICROCLIMATE OF A RELICT STAND OF SUGAR MAPLE IN DEVILS CANYON IN CANADIAN COUNTY, OKLAHOMA[1]

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INTRODUCTION

For several years many workers (Aikman 1931, Broadbent 1950, Champness 1950, Flory 1936, Fredricksen 1938, Noll 1939) have been interested in the effects of cropping on microclimates and the effects of microclimatic factors on crop plants. More recently great interest and research effort has been directed toward the role of microclimates in the distribution of natural vegetation types and individual native species (Christy 1952, Oosting and Hess 1956, Shanks and Norris 1950, Shanks 1956, Vaartaja 1954, Van der Linde and Woudenberg 1951, Wolfe *et al.* 1949). Wolfe *et al.* (1949) indicated the important role of microclimates in determining the distribution of various native species even in a rather small area. Their work stimulated considerable interest in the study of microclimates. Oosting and Hess (1956) compared the microclimate and soil factors of a relict stand of *Tsuga canadensis* in North Carolina with a nearby area in which this species did not occur. They found on the bluff face where Tsuga occurred that insolation, temperatures, and evaporation were lower and soil moisture greater than on the bluff top where Tsuga was absent. They felt that the more mesic conditions on the bluff face enabled Tsuga to survive there, whereas it could not withstand the more xeric conditions of the surrounding areas in which oak-hickory is the climax vegetation. This conclusion agreed with that of Friesner and Potzger (1931, 1934) who considered the Tsuga sites in Indiana to be more mesic than those occupied by oak-hickory vegetation.

The goals of this project were: (1) to determine the range of certain environmental conditions under which a relict stand of sugar maple and several other eastern species of plants are growing in a canyon in west central Oklahoma, and (2) to compare certain environmental factors in the canyon with the same ones outside to help explain why several mesic eastern species have survived in such a dry climate. This study was not concerned with how or why the eastern species migrated into the canyon originally.

The author acknowledges with thanks the assistance of Frank Welbourne, Jr., Don Ahshapanek, and Mohamed Afzal Khan on this project. Thanks are extended also to the Methodist Board

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of Education for permission to carry out the project on land owned by the Methodist Church.

Description of the Area Under Investigation

Devils Canyon is in Canadian County in west central Oklahoma, and is one of a small number of canyons in that general area where *Acer saccharum*[2], sugar maple, occurs. These canyons are about 185 miles west of the typical range of sugar maple in eastern Oklahoma. They have been cut in Rush Springs sandstone of the Whitehorse formation, a poorly cemented, red sandstone of Permian Age.

Devils Canyon is several miles long and 100-200 ft. deep with a soil bottom averaging 354 ft across. The bottoms are bordered by vertical sandstone cliffs 40-70 ft high forming a definite box canyon. In the study area, which is approximately 0.5 mile long, it is impossible to climb out of the canyon without special equipment. The less resistant rock formations above the vertical walls have weathered to form gradually widening, soil covered, vegetated slopes.

The average annual precipitation in Devils Canyon is about 28.5 in., and the average annual evaporation is about three times this outside the canyon.

In this section of Oklahoma and outside the box canyons, tall-grass prairie occurs on soils derived from shales while 3 types of scrubby upland forest communities, blackjack-red cedar, blackjack, and blackjack-post oak, occur on soils derived from sandstone. Rice and Penfound (1959) found that 25 types of upland forest communities occur in Oklahoma.

A recent analysis by Welbourne (personal communication) indicates that scrubby savannah on slopes adjacent to Devils Canyon is of the blackjack-red cedar type (Fig. 1). Blackjack (*Quercus marilandica*) had an importance percentage (average of relative basal area, relative frequency, and relative density) of 57.4, and red cedar (*Juniperus virginiana*) had an importance percentage of 36.9. *Bumelia lanuginosa, Celtis reticulata* Torr., *C. occidentalis,* and *Quercus stellata* occur but are relatively unimportant. The average basal area of the trees is approximately 29 sq. in.

Deciduous forest in the box portion of Devils Canyon is characterized by large, tall trees averaging about 126 sq. in. in basal area and growing 50-70 ft. high, forming a relatively closed canopy (Fig. 2). Welbourne demonstrated that sugar maple is the dominant species with an importance percentage of 22.5. Important secondary species and importance percentages are *Ulmus rubra,* 16.9; *Juglans nigra,* 13.1; *Acer Negundo,* 13.0; *Ulmus americana,* 11.0; and *Celtis occidentalis,* 10.0. A few other tree species occur but are relatively unimportant. Practically no herbs are common to the box canyon and the slopes. Some "outside" species occur in the canyon along a primitive road.

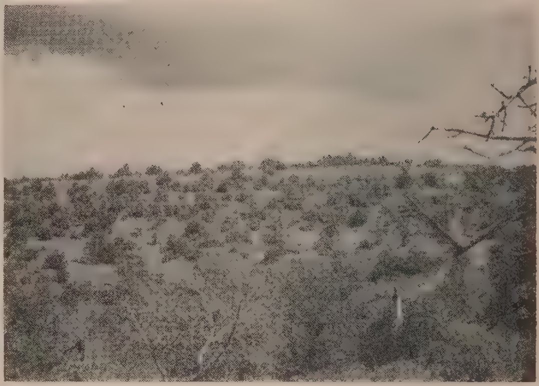

Fig. 1. Scrubby savannah on southeast-facing slope. All photographs taken in July.

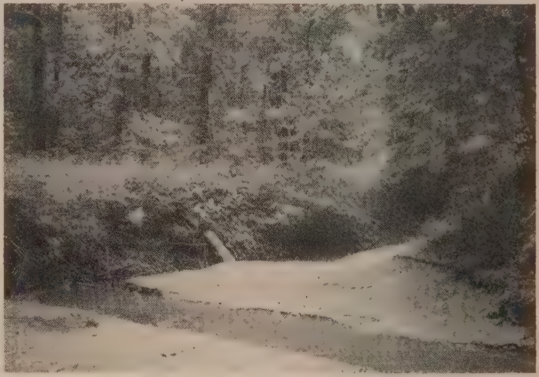

Fig. 2. Forest and small stream in canyon. Stream about 3 feet across.

Several eastern species of herbaceous plants with a disjunct distribution similar to that of sugar maple occur in Devils Canyon. These include *Cryptotaenia canadensis, Erigeron annuus, Laportea canadensis, Osmorhiza longistylis, Panicum boscii,* and *Scrophularia lanceolata. Boehmeria cylindrica* and *Pilea pumila* could possibly be included, although the distance separating these species from their distributional ranges farther east is certainly not as great as for the others.

Several additional eastern species apparently reach the western extent of their range (in Oklahoma) in the canyons of Caddo and Canadian counties. These include *Cinna arundinacea, Elephantopus carolinianus, Leersia virginica, Meloth-*

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[2] Nomenclature follows Fernald (1950) unless otherwise noted.

ria pendula, Menispermum canadense, Passiflora lutea, Polygonatum canaliculatum, Thalictrum dasycarpum, and *Tovara virginiana.*

Based on present knowledge of the upland forests of Oklahoma, *Celtis occidentalis* appears to have a disjunct distribution from that in northeastern Oklahoma. It is possible, however, that this species may occur in bottomland forests in the intervening area.

Probably the sugar maples and other disjunct eastern species are relicts of a more humid period when they could have had a continuous range to the canyons and beyond. It is possible that in a drier climate these small groups of disjunct species survived only in what appear to be more favorable sites in canyon bottoms. Sears (1932, 1933) regarded sugar maples and other disjunct species as relicts of a humid period of 4000 B.C. or earlier. Present geological evidence indicates that Devils Canyon was excavated first during the Pleistocene (Norris 1951). If true, this precludes the possibility of the forest in the canyon being a relict of forests of the Tertiary or Cretaceous periods.

Little (1939) and others postulated that many environmental factors are less extreme in the canyons than outside them. Little states that "Evaporation is much lower and temperatures less extreme in the canyons than in the adjacent upland." This seemed reasonable, but apparently no actual measurements of environmental factors were made.

Measurement and Materials

The following factors were measured at 5 stations in the bottom of the canyon and 5 on the slopes outside the box canyon: air temperature (°F) at 5 ft above ground, relative humidity at 5 ft above ground, air movement at 5 ft above ground, evaporation from white and black Livingston spherical atmometer cups at 5 ft above ground, and soil temperature (°F) at 3 in. depth. In addition, soil moisture measurements of the 0-6 and 18-24 in. levels were made monthly at 10 systematically located positions outside the canyon and 10 inside the canyon. Precipitation was measured by standard weather bureau instruments at 2 stations in the canyon and 2 outside. All temperature and humidity measurements were made by recording instruments, while wind movement was measured by totalizing cup anemometers. Soil moisture measurements were made by determining the water content of oven dried soil samples taken with soil augers.

The canyon is oriented in a generally southwest-northeast direction so the outside stations were located as follows: one at the rim of the box canyon on a northwest-facing slope (Fig. 3), one at the top of the northwest slope, one at the rim of the box canyon on the southeast-facing slope, one at the top of the southeast slope, and one about midway up a south-facing slope. Stations were located with different degrees of shading from the scrubby trees. The canyon-bottom stations were located as follows: one near the northwest wall of the canyon at the upper end of the study area, one near the southeast wall across the canyon from the first mentioned (Fig. 4), one in a cove on one side of the canyon, one in the middle of the canyon, and one on steep talus slope near the northwest wall at the lower end of the study area. These stations were located so that extremes of shading and lighting were encountered in an effort to measure the variability. The hygrothermographs for measuring air temperature and humidity were all in standard weather bureau type shelters.

All instruments were placed in the field on April 12, 1958, except the atmometer cups which were

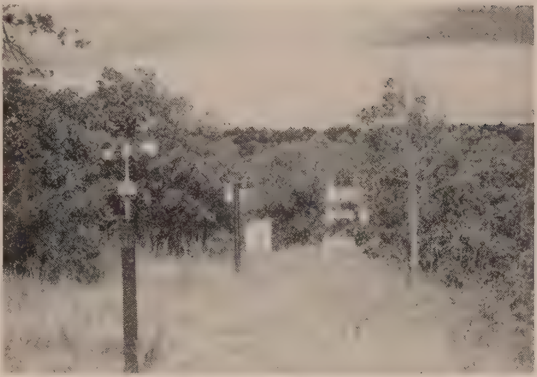

Fig. 3. Upland station at rim of canyon on northwest-facing slope showing anemometer, white and black atmometer cups, soil thermograph shelter (small shelter), and shelter for hygrothermograph.

Fig. 4. Canyon station near southeast wall at upper end of study area showing same instruments and shelters as in Fig. 3.

placed there on May 3 because of the danger of the cups freezing and bursting earlier. Measurements were made until November 1, except evaporation measurements which were discontinued on October 4 because of the possibility of a freeze.

Calculations are based on daily averages for weekly periods. Average daily values of temperature and relative humidity are based on averages of readings taken every 2 hrs. Average daily maximum and minimum values of temperature and relative humidity are based on maximum and minimum values recorded each day. Following the practice of the U. S. Weather Bureau, days were from midnight to midnight.

RESULTS

Air Temperatures

Considering all 5 stations outside the canyon together and all 5 stations inside the canyon together, the average daily minimum air temperature, the average daily air temperature, and the average daily maximum air temperature were consistently higher each week outside the canyon (Fig. 5). Differences were slight in April, during cool spells in the summer, and in late October. The average daily minimum air temperature of the lowest (in temperature) station outside the canyon was consistently lower than the average daily minimum of the highest station in the canyon. The average daily air temperature of the lowest station outside was fairly close to the average daily temperature of the highest station inside the canyon.

The average daily air temperature outside the canyon (average of all stations) was as much as 4°F higher than inside the canyon during some weeks. This does not seem to be a pronounced difference. However, considering the average July temperature at Enid, Oklahoma is only about one degree less than that at Waurika, even though Enid is about 160 miles farther north and at about the same longitude, the difference appears more significant. The average daily maximum air temperature outside the canyon was 6.2°F higher than inside the canyon during some weeks.

The difference between the average daily air temperatures outside the canyon and inside each week was usually significant at better than the one per cent level and the same was true for the difference between the average daily maximum air temperatures. The difference each week between the average daily minimum air temperatures outside the canyon and inside was usually not statistically significant, however.

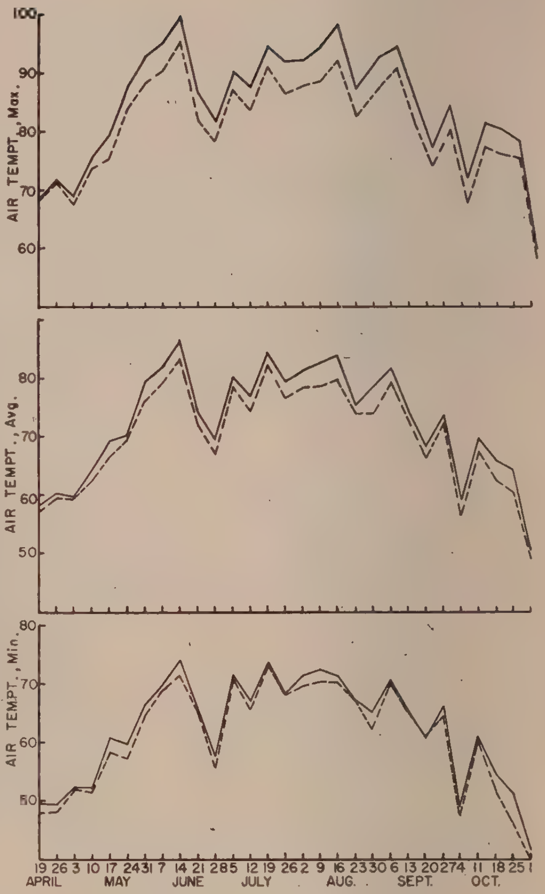

FIG. 5. Comparison of air temperatures (°F.) in canyon (broken line) and outside canyon (solid line) during weeks ending on dates indicated on abscissa. All five stations outside canyon considered together and same for five stations in canyon in this figure and others which follow. Top graph, average daily maximum air temperatures; middle graph, average daily air temperatures; bottom graph, average daily minimum air temperatures.

Average daily maximum air temperatures and average daily minimum air temperatures were similar each month on the slopes outside Devils Canyon and at a nearby U. S. Weather Station (Table I). Average daily minimum air temperatures in Devils Canyon were usually slightly less than in the other localities. On the other hand, average daily maximum air temperatures ran from about 3-5°F lower in Devils Canyon each month than on the slopes or at the weather station.

Relative Humidity

There were no essential differences in relative humidity between the stations outside and inside the canyon during April (Fig. 6). After the first week in May, however, the average daily minimum relative humidity and the average daily rela-

TABLE I. Comparison of average daily minimum and average daily maximum air temperatures for indicated months on the slopes outside Devils Canyon, inside Devils Canyon, and at a nearby U. S. Weather Station

Month	TEMPERATURE—°F					
	El Reno*		On Slopes Outside Devils Canyon		In Devils Canyon	
	Avg. Daily Max.	Avg. Daily Min.	Avg. Daily Max.	Avg. Daily Min.	Avg. Daily Max.	Avg. Daily Min.
May	81.3	58.6	80.9	58.4	77.9	56.7
June	90.1	65.9	91.0	66.8	86.6	65.4
July	91.9	70.3	91.3	70.2	87.2	69.6
Aug.	93.2	68.4	93.1	69.6	87.9	68.0
Sept.	84.2	64.0	85.7	65.9	81.6	65.3
Oct.	75.5	51.0	74.6	51.6	71.3	49.3

* U.S. Weather Bureau Station—Located about 19 miles northeast of study area.

tive humidity were consistently higher in the canyon than outside (Fig. 6). Differences became more pronounced as the year progressed with the greatest differences occurring in late August, September, and early October. The difference between the average daily relative humidity (all stations) outside the canyon and inside during the week ending October 4 was 32.7 (76.6% in the canyon and 43.9% outside).

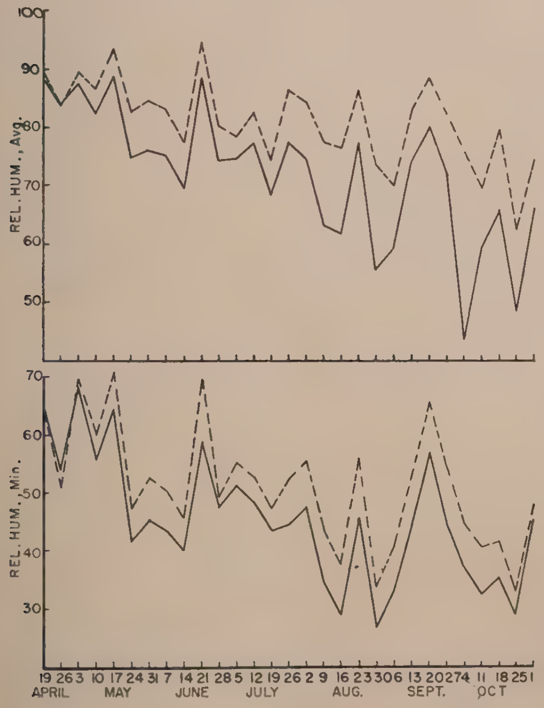

FIG. 6. Comparison of relative humidities (%) in canyon (broken line) and outside canyon (solid line) during weeks ending on dates indicated on abscissa. Top graph, average daily relative humidities; bottom graph, average daily minimum relative humidities.

TABLE II. Comparison of average daily maximum relative humidity in canyon and outside for each week of sampling period. All five stations outside canyon were averaged together and the same for five stations inside

Week Ending On	AVERAGE DAILY MAXIMUM RELATIVE HUMIDITY (%)	
	Canyon	Outside
April 19	100	100
April 26	100	100
May 3	100	99.9
May 10	100	100
May 17	100	100
May 24	100	100
May 31	100	99.6
June 7	100	100
June 14	99.9	98.8
June 21	100	99.6
June 28	99.8	97.8
July 5	98.3	96.9
July 12	99.4	97.9
July 19	99.2	96.4
July 26	100	98.5
August 2	99.2	94.6
August 9	99.8	93.7
August 16	99.8	95.7
August 23	100	97.3
August 30	99.8	89.0
September 6	98.0	91.7
September 13	98.3	97.5
September 20	100	96.8
September 27	100	96.3
October 4	93.7	91.4
October 11	92.0	85.5
October 18	100	94.9
October 25	97.8	80.3
November 1	97.2	89.2

Difference between mean daily relative humidities in the canyon and outside each week was generally significant at better than the one per cent level after the middle of May; this was true also for the difference between mean daily minimum relative humidities.

The average daily maximum relative humidity was high at all stations throughout the study (Table II). It was slightly lower outside the canyon than inside after June 28, and the differences were fairly pronounced in October.

Air Movement

The average daily air movement was from 3.5-15 times as high each week outside the canyon as inside (Fig. 7). The station with the lowest average daily air movement outside the canyon consistently had a considerably higher average than the station in the canyon with the highest average daily air movement.

Evaporation

The average daily evaporation from white spherical Livingston atmometer cups (average of

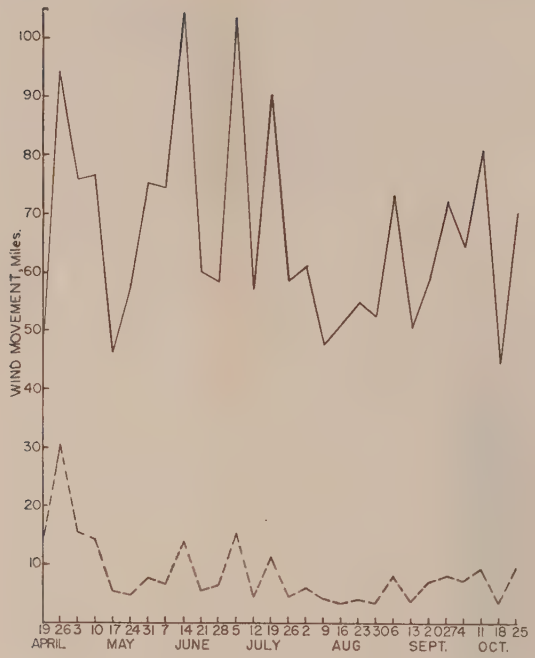

FIG. 7. Comparison of wind movement (average miles per day) in canyon (broken line) and outside canyon (solid line) during weeks ending on dates indicated on abscissa.

all stations) measured from 2-4 times higher each week outside the canyon than inside (Fig. 8). The station with the lowest average daily evaporation (white cups) outside the canyon had a consistently higher average water loss than the station in the canyon with the highest average daily evaporation.

The annual evaporation in this section of Oklahoma is about 3 times the amount of precipitation. Data from this project indicate that evaporation in the canyon would about equal precipitation. General precipitation/evaporation ratios of 1 do not occur in Oklahoma.

During the study, average daily water loss from black cups was 30.1% higher than from white cups outside the canyon. In the canyon, the loss from black cups was only 18.7% higher than from white cups. This indicates that the average insolation on the slopes outside the canyon was considerably greater than in the canyon.

Soil Temperature

The average daily soil temperature and the average daily maximum soil temperature at 3 in. (average of all stations) were consistently higher each week outside the canyon than inside (Fig. 9). The average daily minimum soil temperature was consistently higher outside the canyon than inside

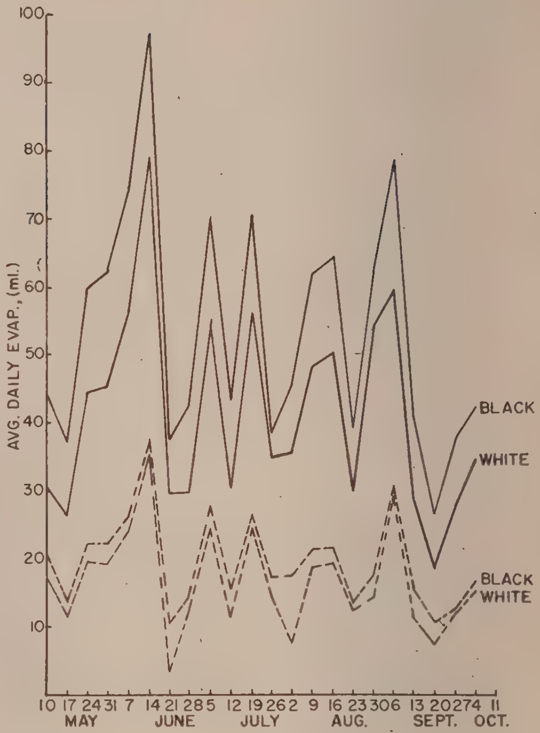

FIG. 8. Comparison of evaporation (average ml. per day) from white and black spherical Livingston atmometer cups in canyon (broken lines) and outside canyon (solid lines) during weeks ending on dates indicated on abscissa.

also, except during April (Fig. 9). The average daily soil temperature outside the canyon (average of all stations) ran as much as 16.9°F higher than in the canyon during some weeks. The average daily maximum soil temperature outside the canyon ranged from 9° to 30° higher than that in the canyon each week.

The difference between the average daily soil temperature in the canyon and that outside each week was generally statistically significant at a high level. This was true also of the difference between the average daily maximum soil temperatures, and usually for the difference between the average daily minimum soil temperatures after about May 1.

Precipitation

Four rain gauge stations were distributed over the study area to obtain data on precipitation during the study period. Precipitation in the area was considerably below normal in May, September, and October. Total precipitation during June, July, and August was almost twice normal, however. During these summer months some rain-

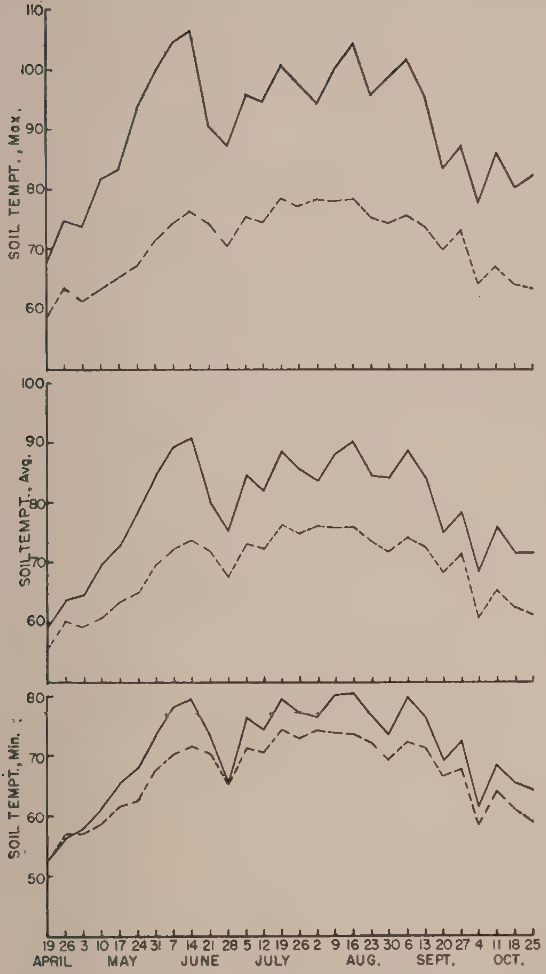

FIG. 9. Comparison of soil temperatures (°F.) in canyon (broken line) and outside canyon (solid line) during weeks ending on dates indicated on abscissa. Top graph, average daily maximum soil temperatures; middle graph, average daily soil temperatures; bottom graph, average daily minimum soil temperatures.

TABLE III. Comparison of weekly precipitation in study area and at U. S. Weather Station at El Reno during study period in 1958

Week Ending On	Precipitation in Inches	
	Devils Canyon	El Reno
April 26	1.22	1.43
May 3	0.10	0.56
May 10	0.18	0.13
May 17	0.20	0.12
May 24	0.02	0.03
May 31	0.46	1.51
June 7	0.11	0.15
June 14	0.49	0.00
June 21	5.53	4.61
June 28	0.22	0.92
July 5	0.30	0.00
July 12	0.81	0.84
July 19	0.22	0.27
July 26	2.46	1.12
August 2	1.84	1.96
August 9	0.06	0.07
August 16	0.08	0.34
August 23	0.19	0.86
August 30	0.92	2.01
September 6	0.00	0.00
September 13	0.46	0.39
September 20	1.07	1.45
September 27	0.36	0.28
October 4	0.02	0.03
October 11	0.00	0.00
October 18	0.02	0.09
October 25	0.00	0.00
Total	17.34	19.17

fall was measured every week, an unusual condition in this part of Oklahoma (Table III).

A comparison of the precipitation each week in the study area with that at the U. S. Weather Station at El Reno, 19 miles northeast, demonstrates the considerable variation which often occurs over short distances (Table III). There were large differences in the amounts of precipitation in the two areas during some weeks, and the total precipitation during the study was almost 2 in. greater at the El Reno station.

Soil Moisture

The unusually high precipitation during the summer of 1958 kept soil moisture fairly high in the study area most of the time. In fact, wet conditions at sampling time precluded soil moisture measurements in June and September. Three sets of measurements, however, were quite interesting. The first was taken on May 24 after about one month during which a total precipitation of 0.5 in. was recorded. This came in light showers scattered through the month. The second set was taken on August 14 after 2 wk during which only O.13 in. of rain fell in two light showers. The third set was taken on October 18 after about 3 wk during which 0.04 in. of rain fell. These measurements demonstrated that the moisture content of the top 6 in. of soil becomes low quite rapidly outside the canyon during a period with little or no precipitation (Table IV). Moreover, the moisture content of the 18-24 in. zone outside the canyon lowers during a short dry period.

DISCUSSION

Results of this project indicate clearly that measured environmental factors are ameliorated in the direction of a considerably more mesic habitat in Devils Canyon as compared with that on the slopes outside the canyon. Air temperature, evaporation, insolation, air movement, and soil temperature were consistently higher outside the

TABLE IV. Comparison of soil moisture (% of oven-dry weight) in canyon and outside for all sampling times. Ten samples were taken at each level outside and ten at each level inside canyon except where indicated differently below.

Date (1958)	Average Soil Moisture (%)			
	Canyon		Outside	
	0-6 inch	18-24 inch	0-6 inch	18-24 inch
April 26*#	15.3	13.8	13.8	17.2
May 24#	8.1	8.8	3.6	6.9
July 10*	17.0	12.7	8.4	7.7
August 14	8.4	11.4	3.6	7.1
October 18	9.4	9.4	3.7	3.8
All sampling times	11.6	11.2	6.6	8.5

* Data obtained during fairly wet period.
# Five samples at each level outside canyon and five at each level inside.

canyon than inside. Relative humidity, on the other hand, was generally higher in the canyon. Soil moisture was depleted much faster outside the canyon.

Stearns (1958) demonstrated that the best single environmental factor correlation with soil water loss was that of soil temperature. Evaporation and solar radiation had a high correlation with soil water loss also. Considering, therefore, that average soil temperature, rate of evaporation, and solar radiation were higher outside the canyon than inside, it is easy to understand why the soil moisture content was lowered at a faster rate outside the canyon than inside.

Shimek (1911) and Transeau (1935) stressed the probable importance of evaporation in the determination of the distributional range of forest versus grassland. Present evidence indicates that the precipitation/evaporation ratio is about 1:1 in Devils Canyon and approximately 1:3 in the general area outside the canyon. The higher P/E ratio in the canyon indicates a greater supply of available water there than outside the canyon. This may be important to the survival of sugar maple and other eastern species in the canyon. It should be pointed out that all other atmospheric factors measured strongly influence evaporation. Considering the fact that air movement, insolation, and average air temperature were consistently higher outside the canyon whereas average relative humidity was generally lower there, it is understandable why the rate of evaporation was higher outside than inside the canyon.

During unusually moist, cool periods the differences in most factors measured were not very great between the inside and outside of the canyon. In relatively dry, hot periods all differences were quite pronounced, however. The summer of 1958 was unusually wet and cool around Devils Canyon; precipitation during June, July, and August was about twice normal. This was reflected in the high soil moisture content and in the high relative humidities which prevailed through the summer. The average daily maximum relative humidity remained close to 100% all summer even outside the canyon. It is possible that in 1958 sugar maple and other eastern species would have survived and grown well even on upland areas outside the canyons. It is unlikely, however, that such species would survive on the upland areas near Devils Canyon during summers with below average or average rainfall. It seems probable that sugar maple would survive in ravines and along streams outside the deep canyons in Canadian and Caddo Counties if it were not for the occasional extremely dry summers there. It appears likely that the pronounced ameliorating effects of the canyons on environmental stresses during periods of drought and high temperature are probably most important in the survival of eastern species of plants in the canyons.

It has been suggested to me that survival of eastern species in the canyons might be due almost entirely to a greater ground water supply and not to any microclimatic factors. The water table is closer to the surface in the canyons than outside, and this probably is involved in the survival of eastern species. It does not appear to be the determining factor, however, as sugar maples and other disjunct species do not occur along ravines and streams outside the canyons where ground water supplies are plentiful. The sugar maples seem to be shallowly rooted in the canyons and, hence, during droughts when the surface layers of the soil are dry, the amount of water available to the roots is probably not great even in the canyons. The apparent role of microclimatic factors becomes evident also when one considers the height of trees in the box canyons. The trees grow upward until the tops reach just slightly above the height of the vertical walls. It appears, therefore, that increased environmental stresses prevent any further upward growth of the trees.

SUMMARY

1. Measurements were made of air temperature, relative humidity, wind velocity, and evaporation from white and black spherical atmometer cups at 5 ft above ground at 5 stations in Devils Canyon and at 5 stations on the slopes outside the canyon. Soil temperature was measured at 3 in. depth at the same stations and precipitation was measured at 2 stations in the canyon and 2 outside. Soil moisture determinations were usually

made each month at 10 stations in the canyon and 10 outside. The sampling period was from April 12 to November 1, 1958.

2. The average daily minimum air temperature, the average daily air temperature, and the average daily maximum air temperature were consistently higher outside the canyon.

3. Precipitation was almost twice the average amount in the study area during the summer months. It was below average in May, September, and October.

4. After the first week in May, the average daily minimum relative humidity and the average daily relative humidity were consistently higher in the canyon. The average daily maximum relative humidity was high at all stations throughout the study.

5. The average daily air movement was from 3 ½-15 times as high each week outside the canyon as inside.

6. The average daily evaporation from the white cups measured from 2-4 times as high each week outside the canyon as inside. Evidence now available indicates that the precipitation/evaporation ratio in the canyon is probably about 1:1, whereas it is about 1:3 outside the canyon. The average insolation on slopes outside the canyon was considerably greater than in the canyon as indicated by a comparison of the water loss from the white and black cups in each area.

7. The average daily soil temperature and the average daily maximum soil temperature at 3 in. depth were consistently higher each week outside the canyon. The average daily minimum soil temperature was consistently higher outside the canyon except during April.

8. The soil moisture content of the top 24 in. of soil was found to lower much more rapidly on slopes outside the canyon than inside during periods with little or no rain.

9. The pronounced ameliorating effects of the canyon on environmental stresses during periods of extreme conditions are probably important in the survival of sugar maple and other eastern species of plants.

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PHYSICAL SITE FACTORS INFLUENCING ANNUAL PRODUCTION OF TRUE MOUNTAIN MAHOGANY, *CERCOCARPUS MONTANUS*[1]

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Introduction

True mountain mahogany (*Cercocarpus montanus* Raf.) is a widely distributed browse species of major importance in the western United States. The palatability is good to excellent for all classes of livestock and it is one of the most valuable winter foods for deer and other herbivorous big game animals. Fundamental knowledge of the ecology of this browse plant is extremely limited. Increasing emphasis on the maintenance and manipulation of browse ranges requires that basic information be obtained on the plants providing the forage. The purpose of this study was to determine the role of physical site factors which influence the annual production of true mountain mahogany. The investigation was designed to identify the physical site factors significantly influencing the annual production of true mountain mahogany, and to assess the relative importance of these factors.

Site factors are commonly grouped into two primary classifications: living and non-living. The non-living factors may be divided into the broad categories of climate and physiography. This study is concerned with the physiographic factors relating to soil and topography.

For invaluable counsel and direction during the study the author wishes to thank the following individuals: Dr. Lee E. Yeager, Leader, Colorado Cooperative Wildlife Research Unit, Colorado State University; Dr. Harold W. Steinhoff and Prof. Charles Terwilliger of the College of Forestry and Range Management, Colorado State University; Mr. E. H. Reid and Dr. Jacob L. Kovner, Chief, Division of Range Research and Mathematical Statistician, respectively, of the Rocky Mountain Forest and Range Experiment Station; Dr. Elmer E. Remmenga, Director, Statistics Laboratory, Colorado State University; and Dr. John L. Retzer, Staff Assistant, Forest Soils, U. S. Forest Service, Washington, D. C.

Study Area

The investigation was conducted from the Little Hills Experiment Station maintained by the Colorado Department of Game and Fish on the western slope of the Rocky Mountains 20 miles southwest of Meeker, Colorado. The region is one of low, rounded hills dissected by streams and washes that have cut narrow steep-sided valleys or flat-bottomed canyons with steep walls.

Soils are derived from the irregularly bedded sandstones and shales of the Green River formation. Generally, they are shallow, rocky, and without distinct B horizons. Textures are coarse, varying from 4-40% clay.

Climatic conditions are characterized by open, dry winters with most of the precipitation occurring during the spring and fall. Average annual precipitation at the Meeker weather station over a 50 yr. period was 15.86 in. Precipitation during the year of this study, 1958, was below average with 12.63 in. About 55% of the yearly precipitation occurs from April through October. Temperatures are generally favorable for plant growth during this period.

Pinyon pine (*Pinus edulis* Engelm.) and Utah juniper (*Juniperus utahensis* (Engelm.) Lemm.) are the climax overstory plants in the region. Open stands allow intrusions of big sage (*Artemisia tridentata* Nutt.), serviceberry (*Amelanchier utahensis* Koehne, Gottung), true mountain mahogany, snowberry (*Symphoricarpos tetonensis* A. Nels.), bitterbrush (*Purshia tridentata* (Pursh) DC.), Gambel oak (*Quercus gambellii* Nutt.), and other shrubby species.

North-facing slopes are often dominated by the mountain-brush type, while small swales and valley bottoms with deeper soils and more favorable moisture conditions support dense stands of sagebrush. Grasses and perennial weeds form fairly dense understories on these sites. South-facing slopes contrast sharply with opposing slopes and support sparse stands of more arid types of vegetation.

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The region is grazed by livestock during the spring and fall and by deer during the winter.

Procedures and Methods

The investigation was pursued from the spring to the fall of 1958. Field procedures involved collection of physical site-factor and mahogany-response data. Laboratory procedures involved the analysis of soil samples collected in the field.

Investigational Design

Sampling was confined to one sq. mile (Section 24, T 1 S, R 96 W, 6th P.M.) considered vegetatively and geologically representative of the surrounding area. Each mountain mahogany community larger than 0.05 acre (approximate) on the section was located, marked on a large-scale topographic map, and classified into one of the following site categories: (1) excellent, (2) good, (3) fair, (4) poor, and (5) very poor. Classification was based on a general evaluation of the site for mahogany production. A categorical estimate of the grossly visible site factors such as aspect, soil depth, parent material, slope position, and slope gradient was made for each community.

No measurements were made during the mapping and classification phases of the study. The initial classifications were designed to facilitate sampling across the full range of the factors being investigated. Approximately equal numbers of communities were then randomly selected for analysis within each of the 5 site categories. Frequent observations were made as the study progressed on the ranges of values of the individual site factors being measured, after which effort was directed toward sampling site factor values not previously sampled.

A random point within each selected community was located by making an enlarged sketch of the irregular community area and using a dot-grid (Bryan 1943) and a table of random numbers. This point served as the center of a 0.01 acre circular plot, which was the sampling unit used in analyzing the physical site and the mahogany response.

Physical Site-Factors

Field examination of the soil on each plot was by pit and in accordance with standard Soil Conservation Service soil-survey methods (Soil Survey Staff 1951). The total depth of the solum was measured, as well as the depth in inches to the bottom of each recognizable horizon. Parent soil material was identified. Structure, consistency, color, root distribution, and relative per cent of stoniness were examined within each soil horizon. A deviation from standard methods was made for surface stoniness. As used here, the term includes all surface stones 3 in. or more in diameter, plus any exposed bedrock on the plot. Standard methods include only stones 10 in. or more in diameter.

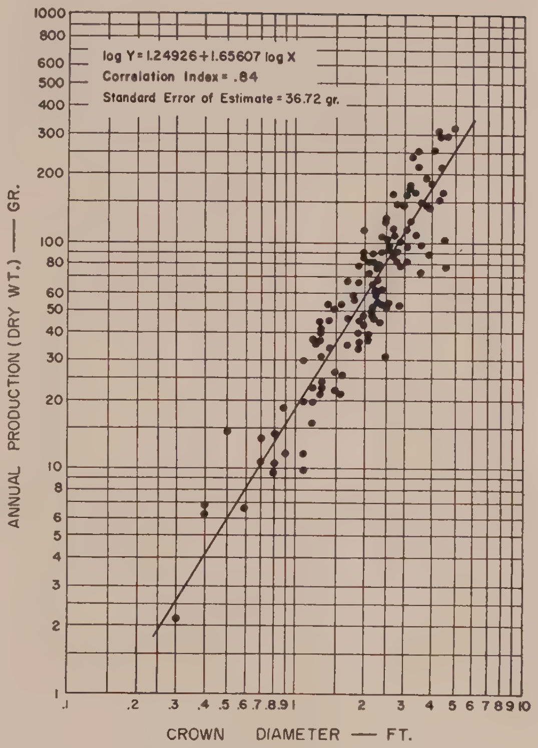

Fig. 1. Relation between air-dry annual production and crown diameter of *Cercocarpus montanus*.

A water infiltration-rate determination (Evanko 1950) was made prior to opening the soil pit.

Topographic features measured on each plot included aspect from true north, average slope gradient, elevation, and position on the slope expressed as the per cent of the distance up the slope to total slope length.

Mountain Mahogany Response

On each 0.01 acre plot the crown diameter of all mountain mahogany plants was measured. After cessation of annual growth, one mahogany plant on each plot was selected randomly for clipping and air-dry weighing of all current annual twig growth. The 125 clipped plants formed a sample of all the mahogany plants in the plots. A regression of dry weight on crown diameter was constructed from the clipped plant measurements (Fig. 1). Annual production was then estimated by regression for each mahogany plant within a plot. These values, summed for each plot and converted to pounds per acre, represented an index of the mahogany response to each site. Predicting annual production from a crown diameter measurement was suggested from the work of Kittredge (1945), who found a similar relationship for two chaparral shrub species in California.

The regression of annual production on crown diameter, shown in Fig. 1 on a double logarithmic scale, was exponential and fitted by the method of least squares. In the equation of the curve, Y is an estimate of the air-dry weight of annual production in grams for a mahogany plant having a crown diameter of X ft. The constants are in logarithmic units.

The use of a regression constructed from a sample of plants from all site classes to predict the annual production of a plant on a particular site is based on the assumption that the annual production-crown diameter relationship is the same regardless of site. To test this assumption, 5 separate regression curves were computed using plants from the 5 categories classified as excellent to very poor. No significant differences were found in either the slope or elevation of the 5 curves.

Laboratory Procedures

Bulk soil samples were taken from the A and B horizons of the soil profile on each plot. Analyses, with the exception of textures, were made by personnel of the Soil Conservation Service Cooperative Soils Laboratory, Colorado State University. Textures were determined by the writer using the hydrometer method of Bouyoucos (1936).

RESULTS

The determination of the relative effects of individual site factors on a unit of vegetation presents a difficult problem of interpretation. Site factors are measured separately in terms of the extent to which each is present on a particular site. In reality, the factors do not function as separate, independent variables, but interact in an intricate maze of interdependent relationships. For interpretation, or partial interpretation, of these relationships, appropriate statistical techniques were used.

Statistical Approach

The analysis was accomplished in 4 parts: (1) the difference in mahogany production on the two parent materials involved, sandstone and shale, was tested for the possible existence of separate populations; (2) individual linear regressions were computed for each independent factor against annual production. (The term "independent factor" is used here in a descriptive manner and does not imply actual independence); (3) interactions among the factors were computed by correlation analyses; and (4) linear multiple regression analyses were then computed combining all the independent factors selected for analysis. Statistical procedures were after Snedecor (1956) and Quenouille (1952).

The following independent factors, applicable to each parent material, were selected for regression analyses:

X_1 = Soil depth (A plus B horizon) in inches.
X_2 = Clay content, A horizon, in per cent.
X_3 = Surface stoniness (stones 3 in. or more in diameter, plus exposed bedrock) in per cent.
X_4 = Aspect, as the sine of the azimuth clockwise from southeast, plus one.
X_5 = Slope position, as the distance up the slope expressed as a percentage of total slope length.
X_6 = Organic matter, A horizon, in per cent.
X_7 = Phosphate (P_2O_5), A horizon, in ppm.
X_8 = Lime ($CaCO_3$), A horizon, in per cent.
X_9 = Infiltration rate, in inches per hour.
X_{10} = Reaction, A horizon, as pH.
X_{11} = Slope gradient, in per cent.
X_{12} = Potash (K_2O), A horizon, in ppm.

The dependent factor "*Y*", is the annual production of mountain mahogany in pounds per acre, air-dry weight, divided by 10. Each dependent observation was coded by a division of 10 to facilitate computations.

Parent Soil Materials

A difference in annual production was found on the two parent soil materials sampled. The 69 sandstone sites had an average production of 169.1 lb per acre. Shale sites, with a sample size of 56, produced an average of 134.3 lb per acre. These two mean values, when subjected to a "t"-test, were found to differ significantly at the 5% level. This difference indicated the existence of separate mountain mahogany populations and necessitated separate handling of the data for each parent material in the further analyses.

Individual Site Factors

Individual site-factor data, separated by parent materials, are summarized in Tables I and II. The results of simple regression analyses (the weight of annual production against each site factor) are indicated by the correlation coefficients. Eight

Table I. Regression-correlation summary, annual production of mountain mahogany (Y) on site factors considered individually (X), sandstone parent material. $N = 69$

Independent factor	Factor mean	Coefficient of correlation	Significant independent factor interactions
X_1 = soil depth (inches)	3.69	.753**	$+X_2$, $-X_3$, $-X_4$, $-X_5$, $+X_6$, $-X_7$
X_2 = clay content, A horizon (%)	16.30	.578**	$+X_1$, $-X_3$, $-X_4$, $+X_6$
X_3 = surface stoniness (%)	11.74	−.498**	$-X_1$, $-X_2$, $+X_4$, $-X_6$, $+X_{10}$, $+X_{11}$
X_4 = aspect (sine of azimuth from S.E. +1)	.8314	−.527**	$-X_1$, $-X_2$, $+X_3$, $-X_6$, $+X_{10}$
X_5 = slope position (%)	47.60	−.339**	$-X_1$
X_6 = organic matter, A horizon (%)	3.91	.397**	$+X_1$, $+X_2$, $-X_3$, $-X_4$, $-X_{10}$
X_7 = phosphate, A horizon (ppm)	12.84	−.313**	$-X_1$
X_8 = lime, A horizon (%)	14.53	−.037	$+X_{10}$
X_9 = infiltration rate (in./hr.)	19.30	−.247*	—
X_{10} = reaction, A horizon (pH)	7.99	−.234	$+X_3$, $+X_4$, $-X_6$, $+X_8$
X_{11} = slope gradient (%)	32.46	−.145	$+X_3$
X_{12} = potash, A horizon (ppm)	55.60	.022	—

** Significant at the 1% level.
* Significant at the 5% level.

Table II. Regression-correlation summary, annual production of mountain mahogany (Y) on site factors considered individually (X), shale parent material. $N = 56$

Independent factor	Factor mean	Coefficient of correlation	Significant independent factor interactions
X_1 = soil depth (inches)	3.02	.709**	$-X_3$, $-X_4$, $-X_5$, $+X_6$, $-X_7$
X_2 = clay content, A horizon (%)	19.00	.089	$-X_7$, $+X_8$, $+X_{10}$, $-X_{11}$
X_3 = surface stoniness (%)	10.73	−.452**	$-X_1$, $+X_4$, $-X_6$, $+X_8$, $+X_9$, $+X_{10}$, $+X_{11}$
X_4 = aspect (sine of azimuth from S.E. +1)	1.2014	−.435**	$-X_1$, $+X_3$
X_5 = slope position (%)	61.23	−.122	$-X_1$
X_6 = organic matter, A horizon (%)	4.53	.346**	$+X_1$, $-X_3$, $-X_{10}$
X_7 = phosphate, A horizon (ppm)	16.23	−.129	$-X_1$, $-X$[illegible], $-X_{10}$
X_8 = lime, A horizon (%)	22.95	−.160	$+X_2$, $+X_3$, $+X_{10}$
X_9 = infiltration rate (in./hr.)	20.84	−.228	$+X_3$
X_{10} = reaction, A horizon (pH)	8.01	−.392**	$+X_2$, $+X_3$, $-X_6$, $-X_7$, $+X_8$
X_{11} = slope gradient (%)	28.30	.039	$-X_2$, $+X_3$
X_{12} = potash, A horizon (ppm)	59.26	−.125	—

** Significant at the 1% level.

of the 12 factors are significantly correlated with annual production on sandstone-derived soils, 5 on shale-derived soils. As might be expected from an environmental analysis, many independent factors are interacting. These were determined by correlating each independent factor against every other independent factor. Only those reaching the 5% level of significance are shown. The signs preceding the factors indicate whether the relationship is direct (positive) or inverse (negative).

The simple correlations, although pointing out isolated relationships, do not contribute greatly to a complete understanding of the site-plant complex. A better understanding can be reached if the individual relationships are examined with a knowledge of the interactions existing. For instance, in graphing annual production against soil depth alone, a misleading interpretation might result unless it were known that the graph includes the combined effects of soil depth and the 5 or 6 (and other unmeasured) factors interacting with soil depth.

Interpretive information is also available from the mean values of the factors. In examining the difference in production between sandstone- and shale-derived soils, the difference in soil depth might be noted. Sandstones, having a greater soil depth, should produce more mountain mahogany. However, the shale sites sampled had a higher average slope position and a greater distribution of plots toward the southwest aspect, both of which are detrimental to increased production. Do sandstone sites truly produce more annual mahogany growth than shale sites? Or is the difference explained by the sampling distribution of plots?

The only conclusion that can be reached here is that under the conditions sampled and at the 95% level of significance, there was a difference in production on the two parent materials.

Combined Site Factors

Multiple regression analyses were used to assess the relative importance of the site factors as they influence annual production. Simple regression analyses, while important in identifying the correlated factors, are not adequate because of the large number of interactions. The partial regression coefficients of multiple regression analysis are based on the effects of any one factor adjusted for the interrelationship with other factors. The linear model used here is:

$$Y \quad b_o + b_1X_1 + b_2X_2 \ldots + b_nX_n + e_{ijk}\ldots$$

where the b's are parameters to be estimated and the e_{ij} are independent normally distributed random variables with mean zero and common variance O^2 (Snedecor 1956).

Procedures for solving the equation were after Quenouille (1952). In this method the relative importance or contribution of a particular independent factor is estimated by the amount of total variation in Y accounted for by that factor at each step in the solution. Four of the factors selected for analysis—soil depth, clay content of the A horizon, organic matter, and aspect—showed non-linear relationships. Aspect was converted to linearity using a sine transformation (Gaiser 1951). For the remaining factors the improvement of the correlation coefficient in fitting a curved line to the data, using a logarithmic transformation, was so small that linear, non-logarithmic relationships were used.

Two solutions of the regression equation, applying different paths of entry, included all 12 of the independent factors selected for analysis. Using these solutions as a basis for judgment, the following factors were subjectively estimated to be only weakly influencing annual production:

On sandstone-derived soils,
X_5 = slope position.
X_6 = organic matter, A horizon.
X_9 = infiltration rate.
X_{10} = pH, A horizon.
X_{12} = potash, A horizon.
On shale-derived soils,
X_7 = phosphate, A horizon.
X_9 = infiltration rate.
X_{10} = pH, A horizon.
X_{11} = slope gradient.
X_{12} = potash, A horizon.

The remaining factors were subjected to further multiple regression analyses. Results are in Table III.

TABLE III. Relative contribution of site factors to variation in annual production of mountain mahogany as estimated by multiple regression analysis

Independent factor	Partial regression coefficients		Standard errors		Sum of squares accounted for by each factor
Sandstone Parent Material					
X_1 = soil depth (inches)...	b_1	−1.18302	s_{b1}	.28872	2266.7**
X_2 = clay content, A horizon (%)...........	b_2	.53720	s_{b2}	.13544	625.9**
X_3 = surface stoniness (%)	b_3	− .11048	s_{b3}	.05235	117.9*
X_8 = lime, A horizon (%).	b_8	− .09335	s_{b8}	.07138	48.2
X_7 = phosphate, A horizon (ppm)................	b_7	− .12788	s_{b7}	.12669	31.9
X_{11} = slope gradient (%)...	b_{11}	.02320	s_{b11}	.04278	7.2
X_4 = aspect (sine of azimuth from S.E. +1).....	b_4	.37901	s_{b4}	1.2241	2.8
Total sum of squares accounted for by regression.......					3100.6
Total sum of squares of Y..........................					4931.0
Constant (b_o) = +7.01 R = .80					
Shale Parent Material					
X_1 = soil depth (inches)...	b_1	1.27039	s_{b1}	.23256	953.5**
X_3 = surface stoniness (%)	b_3	− .08907	s_{b3}	.02820	99.0*
X_6 = organic matter, A horizon (%)............	b_6	.39961	s_{b6}	.31342	18.3
X_4 = aspect (sine of azimuth from S.E. +1).....	b_4	−1.27458	s_{b4}	.99146	15.5
X_8 = lime, A horizon (%).	b_8	.04705	s_{b8}	.06584	13.3
X_5 = slope position (%)...	b_5	.01447	s_{b5}	.01977	8.0
X_2 = clay content, A horizon (%)...........	b_2	.00749	s_{b2}	.10719	0.2
Total sum of squares accounted for by regression.......					1107.8
Total sum of squares of Y..........................					1896.1
Constant (b_o) = +8.16 R = .76					

** Significant at the 1% level.
* Significant at the 5% level.

The relative importance or ranking of each factor is indicated in Table III by the column headed "Sum of squares accounted for by each factor." Each number in the column is the portion of the total sum squares of Y accounted for by that factor after the effects of the previous factors have been discounted. The 5 factors listed above for each parent material, which were eliminated from further analysis, were considered too weak to be reliable and were lumped as a group having very little influence. Also, little confidence is attached to the positioning of the non-significant factors shown in Table III.

The coefficient of multiple correlation (R) is .80 for the sandstone equation and .76 for the shale equation. By squaring this value, a coefficient of multiple determination (R^2) is obtained, indicating that 64% of the total variation in mahogany production has been accounted for on soils from sandstones and 58% on soils from shale. The total variation accounted for is only that due to the 7 physical site factors operating under the same single-season, climatic influence.

DISCUSSION

Soil depth was by far the most significant measured factor in influencing the annual production of mountain mahogany regardless of parent material. The relationship of soil depth to production is shown graphically in Figures 2 and 3. The importance of the soil depth factor has been reported in many investigations relating environment to plant yields. In timber site-quality studies, Coile

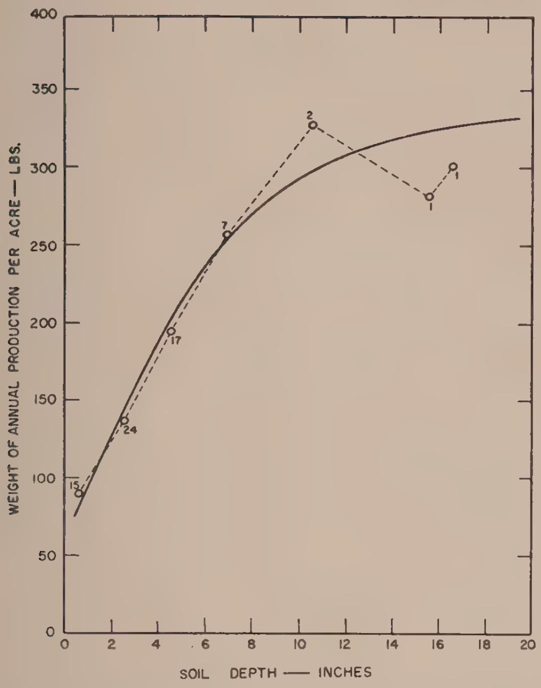

FIG. 2. Relation between weight of annual production and soil depth, sandstone parent material. Plotted points are the weighted averages for two-inch depth intervals.

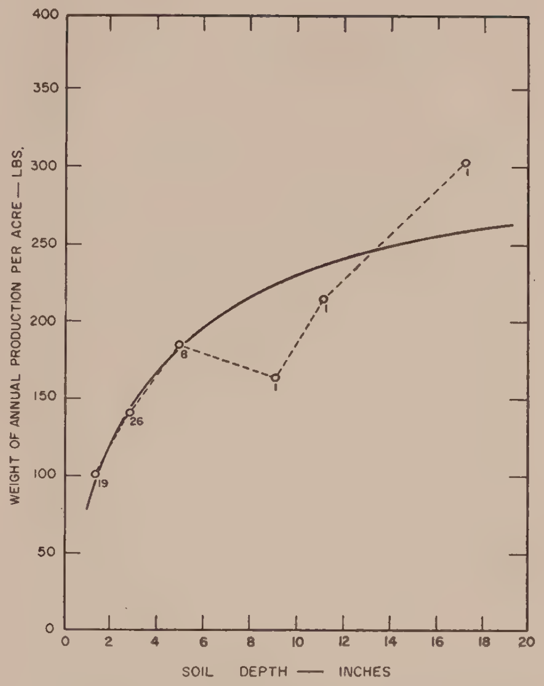

FIG. 3. Relation between weight of annual production and soil depth, shale parent material. Plotted points are the weighted averages for two-inch depth intervals.

(1948), Doolittle (1957), and others have reported positive and significant correlations with soil depth. Similarly, the depth of soil seems to be influential on site potential in range investigations (Retzer 1953, Cronemiller 1955).

Clay content of the A horizon, highly important in sandstone, shows a very low degree of influence in shale soils. This relative lack of importance in shale soils may be explained by the nature of the parent material. Shale is composed of compacted beds of mud or clay, the finest products of rock weathering. Soils formed from such material would be higher in clay- and silt-size particles than soils developed from sandstone. As a result, the clay content of shale-derived soils may be high enough to prevent it from being a significant factor.

Soil depth and the amount of clay profoundly affect the moisture available to plants during the growing season. The greater the depth of soil, and the finer the soil texture, the greater will be the amount of water stored for use by plants. Aeration seems adequate, as the soils considered are light textured and well-drained. Those factors influencing moisture relations, particularly water-holding capacity, appear to be the key ones affecting mahogany yields.

Aspect and slope position, seemingly important from an individual standpoint, did not rank high when combined statistical analyses techniques were used. The influence of these two topographic features is confounded with, and reflected in, the more direct factors of the soil. Even such soil properties as depth and texture are of a secondary nature and have little or no direct effect. These factors are related to plant response through association with the primary factors of water, oxygen, and nutrients (Black 1957).

It is difficult to assign a cause and effect relationship to the influence of surface stoniness. The strong negative relation may simply be a function of the reduced space available for establishment and growth. Mountain mahogany can become established and produce, to a certain degree, in situations of extreme stoniness. However, good stands were never associated with excessive stoniness. The poorest producing sites were those having an exceptional number of stones covering the soil surface.

The relationship between rate of water infiltration and mahogany yield lacked relative importance. Considered individually, negative correlations were found (Tables I and II). Good mahogany sites, associated with deep soils and heavier textures, had slower infiltration rates than poor sites associated with shallow soils and light textures. It is possible that factors related to water retention overshadow in relative importance factors related to an increased rate of water infiltration. The data indicate that this may be so. A more valid explanation may lie in the combination of faulty technique and experimental error. It was impossible to "seat" or "place" the infiltrometer without disturbing the soil, particularly on the rocky soils associated with poor sites. A greater degree of disturbance on poor sites would lead to a more rapid rate of infiltration and, therefore, to a faulty measure. Such experimental errors would be reflected in any statistical treatment applied to the data.

McGinnies and Retzer (1948) have indicated that with some exceptions soil nutrients on western ranges are usually sufficient. Retzer (1954) found little or no increase in native herbage from fertilizer trials in the Rocky Mountains. In my study none of the soil nutrients contributed significantly to variations in mahogany yields. Organic matter showed a certain degree of importance, phosphate and potash practically none. Lime, although high, did not appear to be in excess. Generally, soil nutrients in the area appeared adequate for the requirements of mountain mahogany.

SUMMARY

The relation of certain physical site factors to the annual production of true mountain mahogany (*Cercocarpus montanus*) was investigated near Meeker, Colorado. The study was designed to identify the physical site factors significantly influencing the annual production of true mountain mahogany, and to assess the relative importance of these factors.

Joint observations on site and mahogany stands were made on 125 sample plots, 69 on sandstone and 56 on shale parent soil materials. Plots on soils from sandstone produced an average annual growth of 169.1 lb per acre. Those on soils from shale produced 134.3 lb per acre. This difference necessitated separate handling of the data for each parent material.

Site factors contributing significantly to the variation in current annual production on sandstone-derived soils were soil depth, clay content of the A horizon, and surface stoniness (negatively). Non-significant factors showing moderate importance included lime, phosphate, slope gradient, and aspect. Those factors contributing only very weakly were slope position, rate of water infiltration, organic matter, pH, and potash.

Site factors contributing significantly on shale-derived soils included soil depth, and surface stoniness (negatively). Non-significant factors showing moderate importance were organic matter, aspect, lime, slope position, and clay content of the A horizon. Those factors contributing only very weakly included rate of water infiltration, slope gradient, phosphate, pH, and potash.

Factors influencing soil moisture relations, particularly water-holding capacity, appear to be the key ones influencing the annual production of mountain mahogany. Soil depth was by far the most significant factor regardless of parent material. Clay content of the A horizon was highly important in soils derived from sandstone.

None of the soil nutrients measured contributed significantly to variations in yield. Generally, the nutrient content of the soils examined appears sufficient for the requirements of mountain mahogany.

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THE FOREST SEQUENCE OF THE HARTSTOWN BOG AREA IN WESTERN PENNSYLVANIA[1]

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Introduction

During the past decade an abundant palynological literature has appeared on the bog and lake sediments of the substage intervals of the Wisconsin glaciation, particularly for localities in the New England, Northeastern, and Lake States. Only two bogs in Pennsylvania have been so studied, Bear Meadow in Seven Mountains in the Ridge and Valley Province (Sears 1935) and Glade Run Bog in the Allegheny Mountains Section of the Appalachian Plateaus (Schrock 1945). Both are in unglaciated areas. In view of the important contributions palynology is making to an understanding of forest sequence, climate oscillation, glacier movement, and radiocarbon dating, it was felt that the gap in pollen records for the glaciated portion of Pennsylvania should be filled. The object of the present study, therefore, is to trace and interpret the forest sequence of northwestern Pennsylvania by the pollen stratigraphy of bogs on glaciated terrain. Bogs and ponds near Hartstown, Crawford County, Pennsylvania, were considered suitable for this purpose.

General Characteristics of the Area

The Hartstown Bog Area is east of Hartstown, Crawford County, in northwestern Pennsylvania, south of the eastern arm of Pymatuning Reservoir. It is in the Linesville Quadrangle at 41° 33′ lat and 80° 22′ long (Fig. 1). The bogs are of Wisconsin glacial origin and of the dammed-up-river-bed type (Dansereau and Segadas-Vianna 1952). Following the recession of what was probably the Cary substage (Flint 1947) of the Wisconsin glaciation, a lake of approximately 25 sq miles was left in the Shenango River drainage (White 1881).

Signs of topography modification by glaciation are evident in Crawford County. Preglacial streams of the area have had their original beds buried up to 300 ft by glacial drift and few prominent bedrock outcrops occur anywhere in Erie or Crawford Counties. In the Hartstown Bog Area the drift has formed an almost unbroken series of knolls stretching northwest from Hartstown along the east side of Pymatuning Swamp and Lake to Pennline on the Pennsylvania-Ohio border. These deposits are at right angles to the general trend of the moraine and in coincidence with the general direction of the ice movement, which at this point was from northwest to southeast (Leverett 1902).

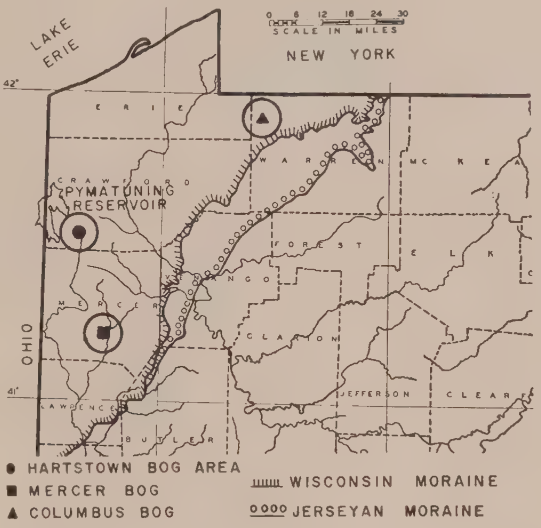

Fig. 1. Map of northwestern Pennsylvania showing locations of bogs studied.

Ecologically, as represented by Braun (1950), this extreme northwestern section of Pennsylvania is just within the eastern border of the Beech-Maple Forest Region, flanked to the north by the Hemlock-White Pine—Northern Hardwoods Region, and to the south by the Mixed Mesophytic Forest Region.

Methods and Procedure

Sampling Sites

Field studies were begun in the early summer of 1955 after a reconnaissance of the area with topographic maps and aerial photographs. Some sampling sites were selected after consultation with J. E. Yewell, Chief Engineer of the Bessemer and Lake Erie Railroad Co. at Greenville, Pennsylvania and R. J. Ferris, Resident Engineer, Pymatuning Reservoir, Jamestown, Pennsylvania,

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[1] Pymatuning Laboratory Publication No. 16. This material was originally presented in partial fulfillment of the requirements for the Doctor of Philosophy degree at the University of Pittsburgh.

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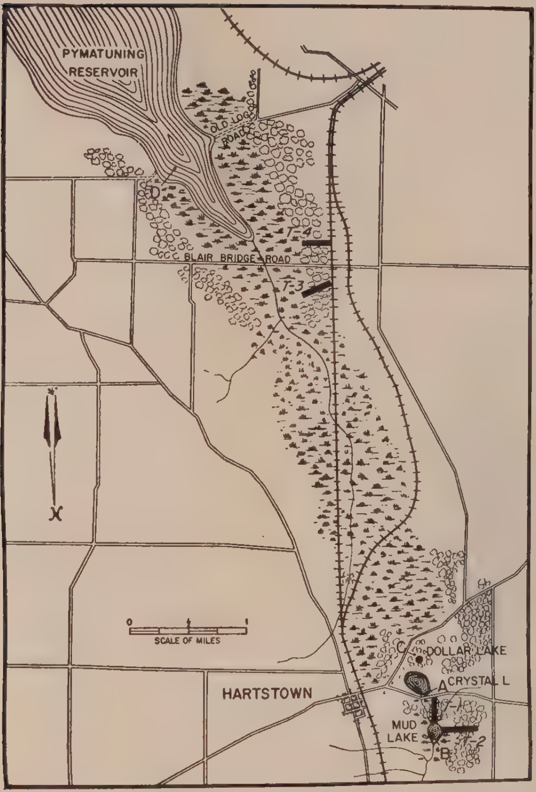

Fig. 2. Map of Hartstown Bog Area showing locations of borings (A, B, C, D) and of transects (T-1, T-2, T-3, T-4).

who were familiar with some of the recognized deeper deposits. The 3 bog ponds at Hartstown, Crystal Lake, Mud Lake, and Dollar Lake (Fig. 2) were selected for deposit sampling because of their depth and the apparent absence of human interference. Another deposit for boring was selected about ¾ miles north of Blair Bridge Road in the Sanctuary Lake portion of Pymatuning Reservoir near the inundated Old Log Road (Fig. 2). To compare and correlate the deeper deposits over a broader geographical area, 2 other Pennsylvania bogs were chosen. One, the Columbus Bog (also called Sulfur Spring Bog), is about 30 miles northeast of the Hartstown Bog Area in the northwest sector of Columbus Township in Warren County just inside the terminal moraine (Fig. 1). The other is Mercer Bog about 27 miles southeast of Hartstown Bog, well within the terminal moraine in northwest Findley Township in Mercer County (Fig. 1).

These sites were picked for the test borings because they were apparently in the deepest deposits under open water and borings could be made through ice in the pollen-free season as advised by Faegri and Iversen (1950). Bog mats were also selected for sampling. During the fall of 1955 and the winter of 1955-56 most of the sample cores for pollen analysis were drilled. The remainder were completed in the spring and summer of 1956.

Pollen and Peat Studies

The sampler used was a Hiller-type peat borer (Faegri and Iversen 1950; Erdtman 1954), manufactured by the Deans Manufacturing Co., Deans, New Jersey. Two 6 in. samples were collected, one from the lower part of the cylinder and one from the upper, and each was put into a separate 40 ml glass vial. Each core was taken in 2 alternate borings about 2 ft apart to avoid contamination. For example, the first foot of sample was taken in core number one, the second foot in core number 2, the third foot in core number one, the fourth foot in core number 2, and so on, alternating down to the earliest post-glacial sediments and subsequently to the original lake bed.

The use of preservatives was unnecessary if the vials were filled with the sample and the caps secured tightly. After storage for 3 months at room temperature, these samples were fresh in appearance and free from mold. In the laboratory each 6 in. sample was thoroughly mixed and a pea-sized lump for deflocculation was removed with a wooden cocktail stirrer. This had a tapered point and could reach to the bottom of the tapered centrifuge tubes for adequate stirring of centrifuged sediments. Since each stirrer was used on only one sample and was discarded at the end of the treatment, such stirrers proved preferable to glass stirring rods or sable brushes in avoiding contamination.

A modified potassium hydroxide treatment described by Sears (1930) and Faegri and Iversen (1950) was used in the deflocculation of most coarse peat and fine peat deposits. For separating and concentrating pollen in some fine peats, the acetolysis method of Faegri and Iversen (1950) was used. If the material contained lime or marl or siliceous matter, the acetolysis method was employed following treatment with hydrochloric and hydrofluoric acids.

After deflocculating the samples and staining the preparation in the last washing with basic fuchsin, the supernatant was decanted and the tube tapped to mix the remaining liquid and the top sediments. A rubber bulb pipette was used to obtain a small drop of this mixture and transfer it to a clean slide on a warming table. A drop of gly-

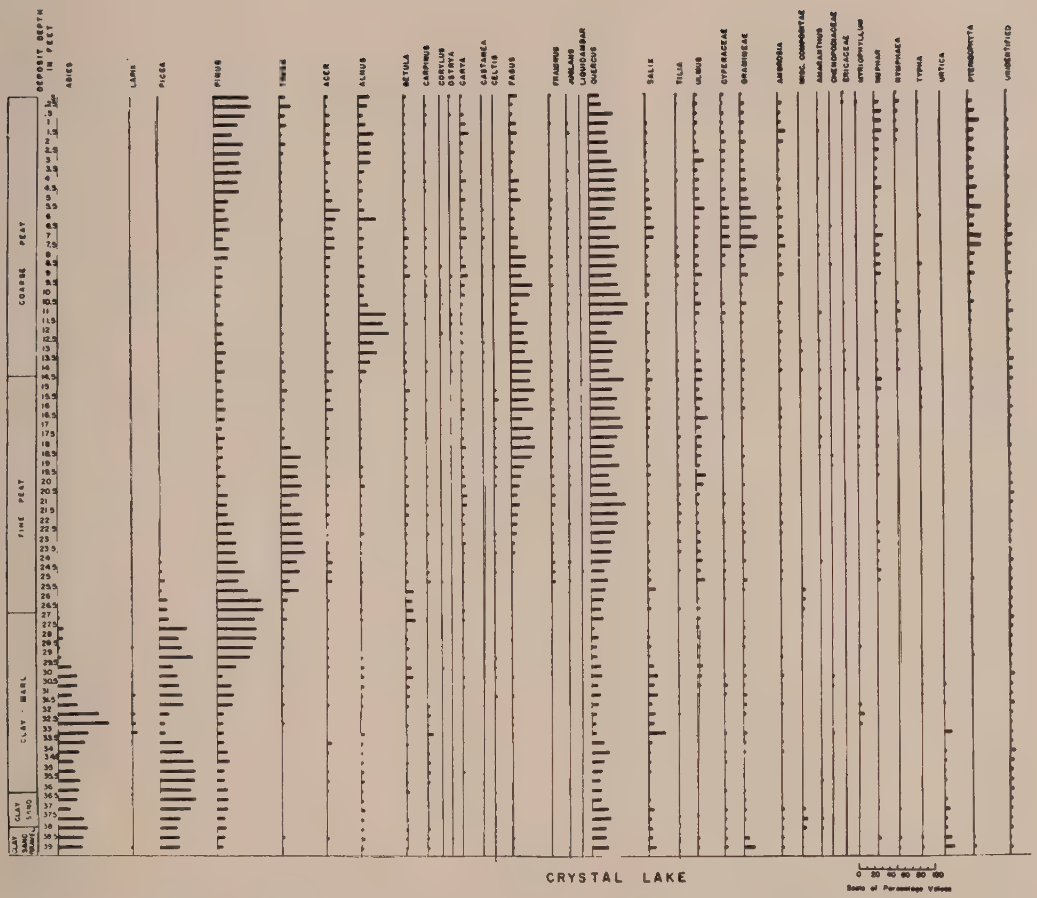

Fig. 3. Pollen diagram for Crystal Lake indicating percentages for various genera based on counts of 200 tree-pollen grains for each spectrum level. Values for non-arboreal pollen and spores are expressed as percentages of total tree pollen.

cerine jelly was added and a cover slip placed over the mixture.

All the samples in each spectrum contained abundant pollen. Two hundred arboreal pollen grains were counted for each unit level in all the pollen diagrams, and the non-aboreal pollen grains were counted and expressed as percentages of the total tree pollen. Counts of 175-200 grains are considered by Barkley (1934) as statistically sufficient to represent the total pollen in any level. Slides were scanned using a binocular microscope until 200 tree pollen grains were identified on each slide representing each 6 in. level.

A slide herbarium was prepared by the acetolysis method from pollen collected in the field during the spring and early summer of 1956 from 69 tree and shrub species and 28 herbaceous species. These slides were the basic reference for the identification of pollen from the bog cores. The works of Sears (1930), Wodehouse (1935), Faegri and Iversen (1950), Erdtman (1952, 1954), and Traverse (1955) were used in pollen grain identification.

Two samples, wood fragments from 39 ft and peat from 26.5 ft from the Crystal Lake diagram (Fig. 3) were dated by C-14 analysis by the Nuclear Science and Engineering Corporation in Pittsburgh. The wood samples were identified after sectioning at 7, 10, and 15 μ, staining in one per cent safranin, and mounting in Canada balsam.

Measurement of Present Plant Cover

In the areas contiguous to the bog samplings the vegetational cover was investigated by a modified line intercept method (Buell and Cantlon 1950). Four line transects (Fig. 2) were run—two from the Mud Lake water margins through the forest zone and two in the Blair Bridge Road forest communities. The percentage of tree and

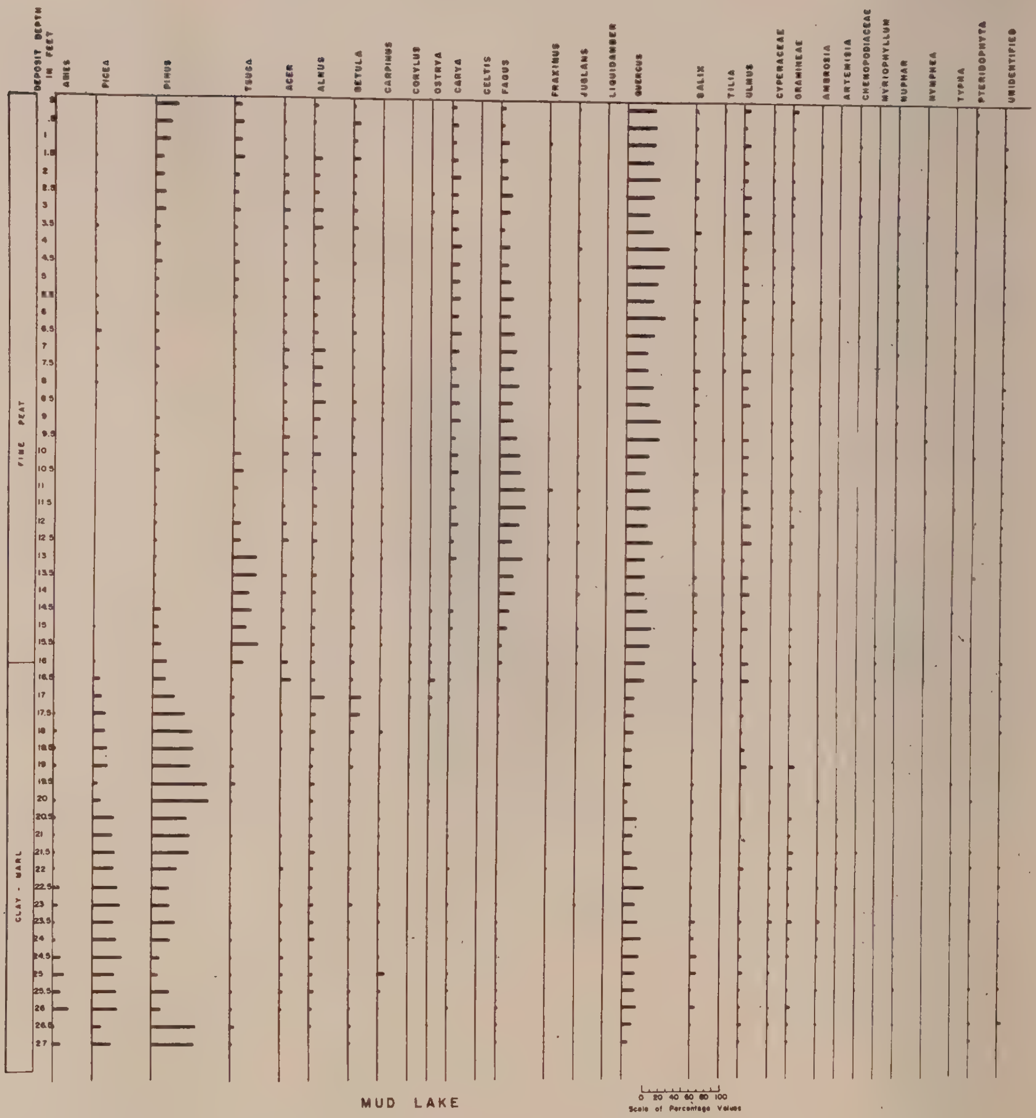

FIG. 4. Pollen diagram for Mud Lake. Percentage values calculated as in Figure 3.

shrub cover was calculated and the dominant tree species measured. One hundred and seventy vascular plant species were collected and deposited in the Pymatuning Laboratory of Field Biology Herbarium. Nomenclature for all the vascular plants discussed in this paper is according to Gray's Manual 8th ed. (Fernald 1950).

RESULTS

The Pollen Spectra and Trial Borings

Pollen histograms were constructed for the Crystal Lake, Mud Lake, Dollar Lake, and Old Log Road pollen diagrams. (Figs. 3, 4, 5, 6) and will be discussed in that order. A histogram comparing the 38-25.5 ft. levels and the 12 and 10.5 ft. levels of Crystal Lake with the Mercer Bog 38 and 37.5 ft. levels and 12 and 11.5 ft. levels respectively, and comparing the 23-21.3 ft. levels in Columbus Bog with the deepest sediments in the other 2 was constructed for profile study (Fig. 7).

Four trial borings were made through the ice at Crystal Lake before the deepest deposit (A) was found (Fig. 2). The 4 trial borings were under 18, 12, 15, and 7 ft. of water respectively and proved to be comparatively shallow sediments ranging from 3-7 ft of peat over clay. These were taken, together with the preliminary diagram, in

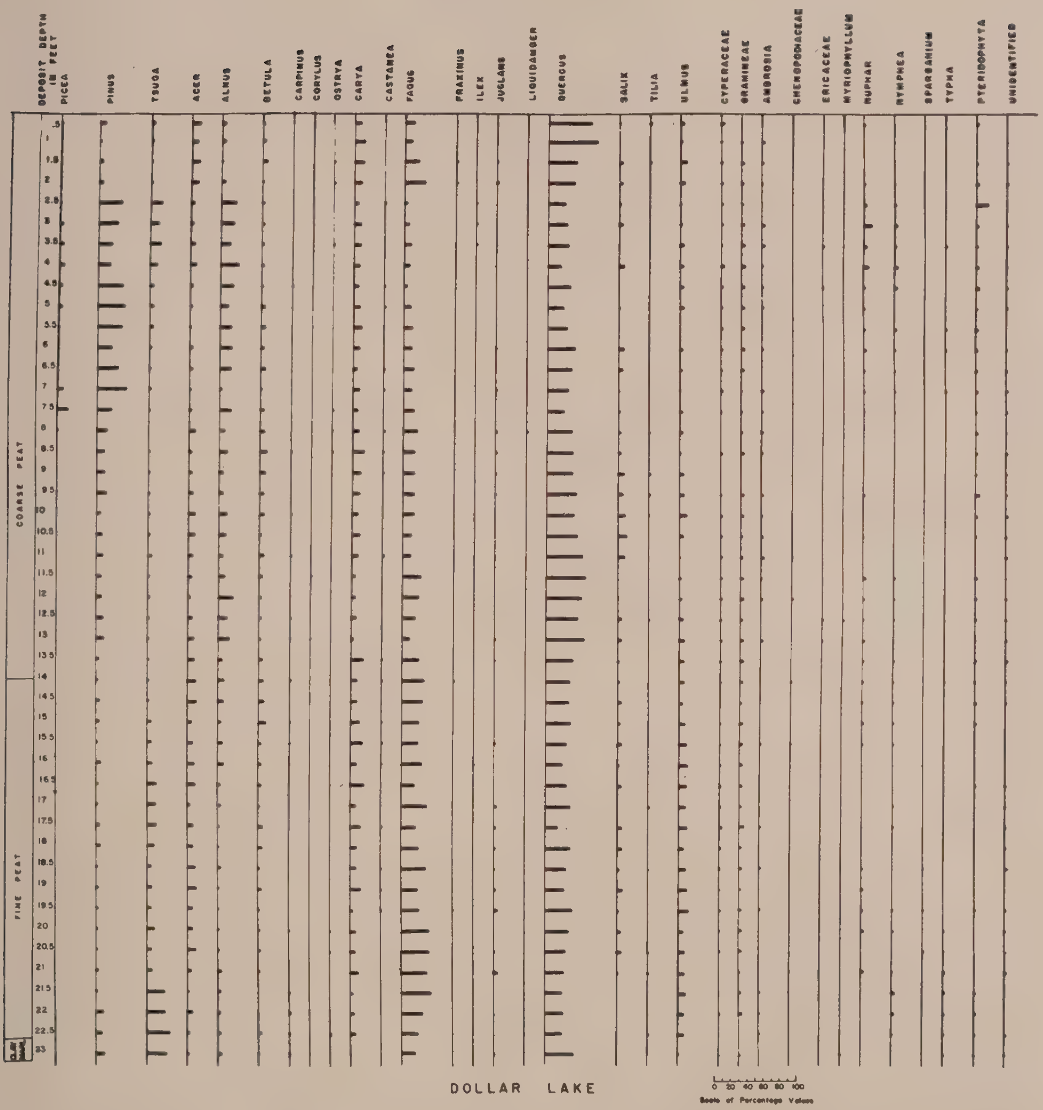

FIG. 5. Pollen diagram for Dollar Lake. Percentage values calculated as in Figure 3.

February, 1956. The complete column for analysis (A) was taken on April 23 and 24, 1956, when the maximum temperature was 44°F and the minimum 29°F with calm air movements. The pollen rain was at its minimum with hazel, alder, willow, poplar, and elm well past their maximum production. No other deciduous species or conifer had shed pollen this early. Extreme care was taken to prevent contamination with contemporaneous pollen in the sampling of this column.

Two trial borings through the ice were made in Mud Lake (Fig. 2) prior to the discovery of the deep (B) stratification. The first trial boring was under 5 ft of water and yielded 6 ft of peat before striking clay. The second trial boring was on the edge of a Decodon mat and was about 40 ft in depth. The deposit in this area contained two water pockets, one at the 11 ft and another at the 20 ft level. The deposit eventually selected (B) was 27 ft deep and under 11 ft of water. It was drilled in June, 1956, from a floating anchored platform.

Of the 3 ponds (Fig. 2), Dollar lake is the deepest but the smallest in surface area. At the center of this diminutive, 200 ft diameter pond, 30 ft of instrument rods was required to reach the surface of the deposit. Since the total rod length carried with the instrument was only 46

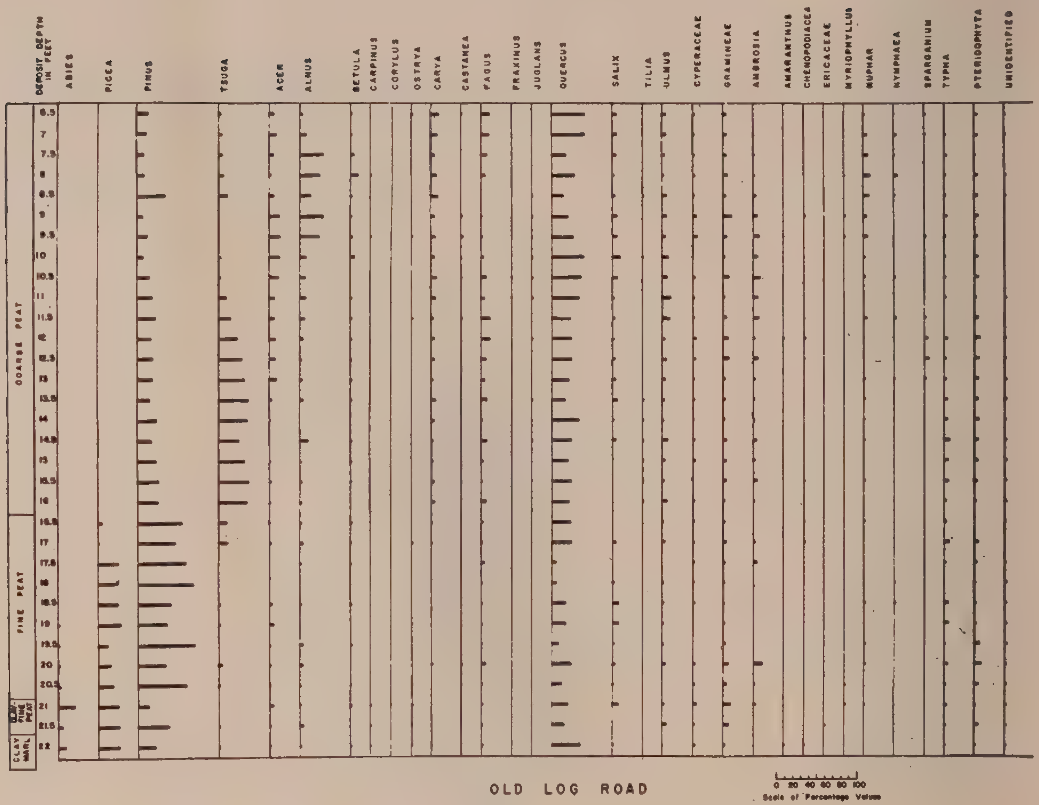

Fig. 6. Pollen diagram for Old Log Road. Percentage values calculated as in Figure 3.

ft, a representative sample could not be taken. Two trial borings were unsatisfactory because of water pockets in the deposit. At (C), a location back from the edge of the water in the Alder zone, a continuous column to 23 ft was sampled. Alder and Swamp Willow formed a continuous growth to the edge of the water completely encircling the pond. Off this Alnus-Decodon mat the water depths averaged 15 ft and the bottom profile angled sharply to the center depth of 30 ft. Suspicion that his site had been subjected to frequent changes in the water table and possible redeposition of sediments was confirmed subsequently in the construction of the histogram.

The Old Log Road samplings were taken through ice on February 6 and 7, 1956 (Fig. 2). The two test borings were too brief to be significant. The sample taken was under 5.5 ft of water in Sanctuary Lake (D) and reached a core depth of 22 ft.

Crystal Lake Diagram

From the criterion of depth, the core of the Crystal Lake boring was apparently the most complete deposit of the 3 sampled, as reflected by the pollen stratigraphy (Fig. 3). The bottom foot of this core was in clay mixed with some sand and angular pieces of gravel. In 7 separate shots into this lowest level in an attempt to obtain at least the minimum wood fragments required for C-14 dating, the strain on the rod coupling, 3 sections above the sampler, sheared the case-hardened bolt at the union, and the remaining rods were withdrawn without the sampler. At 39 ft, including 12 ft of resistant clay, the sampler was permanently lost. Preliminary caution while assembling the peat borer and discarding of any bolt showing the slightest wear should prevent such a costly and time-consuming accident.

There are 3 levels in the Crystal Lake core, clearly distinguished by their color and texture. The top layer down to 17 ft is reddish brown and contains considerable macroscopic vegetative debris. This includes minute particles of sphagnum moss leaves, conifer needles, seed coats, and grass and sedge leaves, and larger fragments of roots, rhizomes, and woody stems. Dark-brown granular humified peat is found from 17-27 ft, while the layers below this are adhesive marl and blue clay,

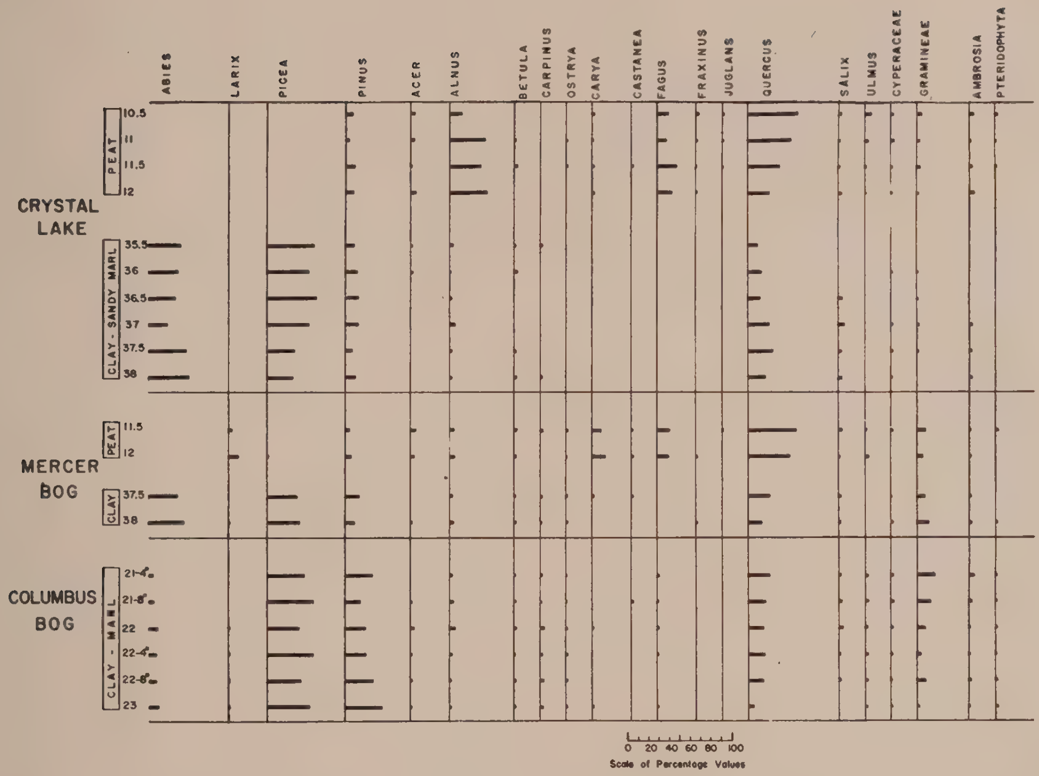

FIG. 7. Comparison of pollen profiles at specific depths among three northwestern Pennsylvania bogs.

with sand and angular gravel particles mixed in at the lowest level.

This pollen diagram correlates in a very general way the findings of Sears (1930a), McCulloch (1939), Voss (1939), Potzger (1943, 1956), Krauss and Kent (1944), Deevey (1951), and Niering (1953). The pattern is that of an initial fir-spruce-oak-pine forest followed by a pine dominated forest of relatively long duration. This is succeeded by an oak-hemlock stage and a beech-oak stage accompanied by hickory and basswood. The deciduous complex continues with an increase in pine and hemlock and a decrease in oak.

Although the general pattern of this diagram agrees with that established by the authors listed above in its general forest sequence, it is not identical with any of them. In deposits where the first vegetational records were preserved after the last ice retreat, there is a small percentage of larch, birch, hornbeam, and beech, a slightly larger amount of elm and alder, and a significant amount of willow. In the non-arboreal pollens the chief herbaceous forms in this first record are grass, nettle, and sedge. Pine remained an accessory species during the spruce-fir period. Fluctuations of the two dominant species occurred with spruce and fir showing two alternating periods of dominance. No fir appears in the diagram above the pine maximum at 26.5 ft, and the last two pollen grains of spruce are found at 24.5 ft in the column. Pine pollen counts are diminishing at this point too, although they remain in the stratigraphy throughout every level, as does oak.

Two sizes of Pinus pollen grains were observed. The larger, up to 80 μ in diameter, is more frequent from the beginning to the first pine maximum in the diagram. The smaller, 48μ, is more frequent above the first pine maximum. No attempt was made to identify these as to species, but several workers have reported two or more sizes of pine pollen in their analyses (McCulloch 1939, Cain and Cain 1948, Potzger and Tharp 1954, and Frey 1951).

Acer, Carpinus, Salix, Urtica, and Betula become a little more prominent in the first spruce maximum. Carpinus is prominent from the first spruce maximum to the last fir maximum. Birch reaches its maximum along with pine and continues in low numbers to the present with another slight maximum in the 9.5-7.5 ft levels. Alder and oak increase significantly during the period marked by a slight drop in beech, maple, and basswood.

TABLE I. Results of measurements of vegetative cover along transects through bog and forest communities. Values represent percentage of cover occupied by each species along a transect line

Trees and Shrubs	Mud Lake T-1 North	Mud Lake T-2 East	Blair Bridge T-3 S. West	Blair Bridge T-4 West
Acer rubrum	51.9	48.1	8.5	29.9
Acer saccharum				3.7
Alnus rugosa	2.8		64.8	
Amelanchier canadensis	8.8			
Betula lutea		29.1	8.9	10.4
Carpinus caroliniana			1.7	8.8
Carya glabra				3.4
Carya ovata				6.8
Celtis occidentalis		1.0		
Cornus amomum			11.1	
Cornus racemosa			1.8	
Cornus stolonifera			9.4	
Crataegus (Coccinea Gr.)				1.1
Fagus grandifolia				6.2
Fraxinus americana				9.4
Fraxinus nigra	5.6		6.1	4.2
Hamamelis virginiana		1.4		1.2
Ilex verticillata			6.1	
Juglans cinerea		2.7		
Juglans nigra				3.0
Larix laricina	21.2			1.9
Lindera benzoin			1.8	
Liriodendron tulipifera				0.9
Magnolia acuminata		1.0		
Nyssa sylvatica				0.4
Ostrya virginiana				6.4
Pinus resinosa				0.8
Pinus rigida				3.5
Pinus strobus	2.6	10.1	4.8	1.4
Populus grandidentata		6.5		6.2
Prunus pensylvanica	25.8	2.2		3.9
Prunus serotina		4.0	8.5	8.4
Prunus virginiana		1.4		
Pyrus malus				2.8
Quercus alba				16.0
Quercus velutina				24.1
Rhus vernix	3.7		.8	1.9
Salix lucida			5.8	
Sambucus canadensis			0.6	
Tilia americana	1.7			
Tsuga canadensis		31.2	1.5	12.1
Ulmus americana	13.4	8.9	6.8	2.0
Vaccinium corymbosum			2.4	0.3
Viburnum cassinoides			1.3	
Space	24.3	9.7	27.1	2.3

The beech-hickory complex follows and is later accompanied by a very marked rise in willow, grass, sedge, and fern and fern allies.

Mud Lake Diagram

The deposit at Mud Lake is composed of 11 ft of clay-marl and 16 ft of fine peat. The coarse peat level is missing from this core. This diagram (Fig. 4) is similar to the Crystal Lake diagram in forest sequence, and although it is 11 ft shorter than the latter, it has the same clay depth. The pollen analysis further illustrates a complete diagram, including the same initial species found in Crystal Lake. There is no evidence of truncation here. This comparison indicates variable rates of deposition, which may also occur when two or more borings in the same bog are contrasted (Potzger 1956).

The first forest stage of fir-spruce-oak-pine is present but with an incipient pine maximum and less fir throughout. Spruce has one maximum period only, but reappears in low numbers at the end of the oak-hemlock period and remains well into the mixed deciduous forest. Spruce appears in the upper levels of some of the northern bogs in northern Ohio, Illinois, central New York, Wisconsin, New Hampshire, Maine, and northern New Jersey (Sears 1930a, McCulloch 1939, Krauss and Kent 1944, Potter 1947, Deevey 1951, Niering 1953), but not in the majority of north-central Ohio Bogs (Potter 1947).

The percentage values for fir, pine, oak, hemlock, hickory, beech, birch, maple, elm, alder, and hornbeam are essentially equal in Crystal Lake and Mud Lake diagrams. Willow, ash, basswood, sedge, grass, spatterdock, water lily, and ferns are represented by much lower percentages in the Mud Lake analysis. Larch and stinging nettle are absent. Liquidamber appears as a single pollen grain in several Crystal Lake levels, and in one Mud Lake spectrum. This seems an anomaly so far north of the present range of Liquidamber, but Deevey (1951) reports this species in low pollen percentages from the Maine bogs. In a discussion of the range limits of certain plants in western Pennsylvania, Jennings (1929) traces the course of the northward migration of the Liquidamber associate, pawpaw (*Asimina triloba*). Present day erratic distribution of the pawpaw in western Pennsylvania, eastern Ohio, southwestern New York, and along the south and north shores of Lake Erie, suggests that Liquidamber might have had the same past distribution.

Dollar Lake Diagram

It is obvious from the Dollar Lake diagram (Fig. 5) that its stratigraphy differs from that at neighboring sites (Figs. 3, 4). Physically the boring lacked depth in the initial clay and marl layers, which were impenetrable below one foot. The fine peat was semi-gelatinous and the coarse peat sediments lacked homogeneity.

The distortion is reflected in the values for spruce in the upper regions of the coarse peat. Both pine and hemlock show inverted sequences in the column. The only major deciduous genus that follows the normal pattern is oak. The comparative abundance of hickory and beech pollen in the total stratigraphy suggests an extremely unnatural sequence. This is the only diagram in which holly appears. The non-arboreal pollens are in such low percentages that they have little or no significance.

This diagram is apparently a representation of redeposition and the "water pocket phenomenon" (Faegri 1956, Faegri and Iversen 1950). The shape of the water basin, with steep vertical sides, probably contributed to the secondary deposition through cave-ins of its upper unstable sediments. A boring in the center of the open water might produce a more significant diagram.

Old Log Road Diagram

The stratification of sediments at this site (Fig. 6) was similar to the Crystal lake column, with the exception of a shallower clay layer. The core began at the 6.5 ft level since the upper sediments were flooded. The shorter record of fir and spruce and the early pine maximum probably indicate a slightly truncated diagram when these spectra are compared with the Crystal and Mud Lake borings (Potzger 1956). A deeper penetration should have been attempted to add more records from the clay.

The same initial fir-spruce-oak-pine forest is indicated, but with an earlier pine maximum. The hemlock maximum accompanies oak. This is followed by a shorter hickory-beech period and an increase in oak and pine. Chestnut is absent in the Mud Lake deposits but it occupies the same general spectra in Crystal Lake and Old Log Road coarse peats. Following the beech maximum, alder percentage is high and continues into the mixed deciduous period. A late but brief pine and hemlock maximum accompanies this last phase. The increase in the percentage of the non-arboreal pollen (spatter-dock, water lily, ragweed, and ferns) duplicates the Crystal Lake sediments. The first bur-reed pollen appears in this diagram.

This area is an old bog remnant, its sediments having evidently survived surface draining and flooding caused by the alternating changes in direction of flow of Crooked Creek and Shenango headwaters, which rise at the nearby divide.

Comparison Bottom Profiles

The lower deposits of Columbus and Mercer Bogs, regardless of their depth differences (Columbus, 23 ft; Mercer, 38 ft), are indicative of the same pioneer fir-spruce-oak-pine forest reflected by the Crystal Lake early spectra (Fig. 7). Lower percentages of fir in the Columbus Bog may imply truncation. The boring was made on the mat at some distance from pond-center, but the spruce and pine percentages correlate closely with Crystal Lake and Mercer Bog. The deep boring at Mercer Bog was from the mat and no truncated column is indicated. Larch pollen is present in both the northern and southern bog lower sediments but is absent between the 39 ft and 33 ft levels in the Crystal Lake diagram. Chestnut, hickory, and hornbeam occur in low percentages in Mercer and Columbus Bogs but do not appear in Crystal Lake lower deposits. Beech and elm are in these spectra in Columbus Bog and missing in the other two. Grass is represented in a higher percentage in the two comparison bogs than in the Crystal Lake sediments.

These 3 bogs with an origin dating from the Cary substage retreat in their respective areas but of probably different ages and deposition rates, correlate identically in the pollen analysis of the key forest genera.

Line Transects

The present vegetative cover in the Hartstown Bog Area does not differ generally from that described by Van Dersal (1933). The 1100 ft. line transects, T-1 and T-2 (Fig. 2), at Mud Lake reveal a typical hydrarch succession through the varied seral stages to a swamp forest, and in the direction of a climax beech-maple or hemlock-white pine-northern hardwoods forest. The Blair Bridge Road transect, T-3 (Fig. 2), is 800 ft. long and indicates an initial swamp forest; the T-4 transect in the same vicinity runs 1600 ft. through a patch of modified beech-maple climax forest in a developmental stage. The measurements of shrub and tree cover in these 4 line transects are tabulated in Table I.

DISCUSSION

Forest Sequence and Climate

The forest sequence in the Hartstown Bog area can be divided into 5 major forest progressions related to climatic periods as suggested by Sears (1942). First, the spruce-fir dominance is indicative of a moist, cool period; second, the pine dominant-oak accessory forest suggests a dry, warmer period; third, the hemlock-oak-beech succession followed a climatic swing to a humid, warm period; fourth, the oak-hickory maximum is marked by a warm, dry period; and fifth, the return to a pine maximum accompanied a shift to a cool, moist period. These climatic inferences are based on observations of present-day forest genera and their temperature and moisture tolerances as recorded by Potter (1947), and Braun (1950). A table compiled by Deevey (in Flint

1957) illustrates typical pollen-stratigraphic sequences in northeastern North America. This includes lake and bog profiles from Michigan, southern Connecticut, northern Maine, and central Quebec. With the exception of the Michigan bogs, each profile indicates a park-tundra vegetation following deglaciation. At first glance, it is difficult to infer tundra from the base spectra of Crystal Lake with the obvious prevalence of spruce, fir, and oak. But this might have been a transition zone between a narrow belt of tundra and the open park-tundra of a northward advancing coniferous forest (Livingston 1955). Significant percentages of willow, grass, sedge, ragweed, and nettle pollens in these initial spectra could imply this park-tundra climax stage. The chance of mistaking nettle pollen here for hazelnut pollen (Cain 1939) is slim, since the latter has been recorded at many levels in the diagram. The Mud Lake and Old Log Road initial spectra do not reflect these percentages, but both may have the earliest deposition record missing. Mercer Bog, of comparable deposit depth to Crystal Lake, has the same percentage of grass pollens in the basal stratum. The moderate decrease in willow pollen and in the pollens of the light-tolerant non-arboreal genera, immediately following the initial spectrum, could also indicate a closing forest canopy.

Fluctuation of fir and spruce is probably the result of alternating periods of ice advance and recession. Picea in its present range is slightly more tolerant northward than Abies, but Abies has a more accelerated growth rate and a greater tolerance to root-level water tables than Picea. As in many of the Ohio bogs (Potter 1947), the Hartstown Bog area profiles fail to show spruce in the upper strata. The one exception is Mud Lake, where spruce appears in 13 of the upper levels. In Deevey's composite profile (in Flint 1957) of several northeastern North America bogs and lakes, the occurrence of spruce in the upper strata can obviously be correlated with the location of these bogs and lakes in or near the present day life zones of that conifer. The Ohio bogs and the Hartstown Bog area are no longer refugia for native spruce.

The pine maximum is accompanied by a maximum in birch which is more of a secondary indicator of drying conditions than oak (Potter 1947). The oak increase during the pine maximum is slight, and does not attain its first dominance until after the pine maximum. Several species of pine could be represented in the spectra of all deposits. *Pinus strobus* is usually more plentiful in the upper strata, and *P. Banksiana* and *P. rigida* in the earlier depositions, according to Sears (1942). The smaller pine pollen in the basal Hartstown spectra could be *P. Banksiana.* The birch maximum with this pine in the Crystal Lake and Mud Lake diagrams suggests a mixed jack pine—white birch association similar to some northern New York regional forests of today. These two species have a good tolerance range to the edaphic conditions of coarse and fine glacial till and sandy delta and lake deposits, and to a warmer-dryer climate similar to that of the pine period (Braun 1950). There is a slight elm increase at the end of the pine and birch maxima, probably indicative of the incipient succession to the more humid-warm beech-oak-hemlock period. The segregation of the birch and elm spectra in the diagram might not have been recognized had interval units larger than 6 in. been used. Pollen composition can change rapidly in the vertical borings over short distances and some workers may use half-inch intervals in crucial areas of a core (Frey 1953).

The definite increase and sustained maximum of Tsuga immediately following the pine maximum is the effect of the gradual ameliorating of the climate to the warmer-humid period. Hemlock is prominent in all the Hartstown deposits. However, the movement of Tsuga into a Pinus association is a basic successional behavior pattern for this genus. Since in its present range hemlock demonstrates a decided tolerance to shade but is slow to pioneer into new sites (Hough and Forbes 1943), the period for edaphic and climatic conditions to favor its invasion must have been extensive. Oak is co-dominant with hemlock, and throughout the same spectra there is strong indication of a transitional understory of beech, maple, birch, elm, willow, hackberry, ash, basswood, and hickory. Hickory appears to be a disjunct here, slightly out of its climatic range, but since it can exist in climates with sharp variance from its optimum, it cannot be used as the best index relating to climatic change (Dansereau 1957). Deevey (in Flint 1957) divides the warm-humid period into an oak-hemlock and an oak-hickory forest succession, with a first beech maximum accompanying the latter in the Michigan and southern Connecticut deposits. A second beech maximum occurs in these areas along with oak-elm-chestnut and maple. There is a definite first and second beech maximum of this type in the Crystal Lake and Mud Lake profiles. The first beech maximum is associated with the oak-hemlock and hickory forest of the warm-humid period, and the second beech maximum occurs with the lower spectra of the oak-hickory forest in the warm-dry period. Beech comes into its first maximum following the decline of hemlock. According to Hough and Forbes (1943) beech is the most ubiquitous hardwood on the Pennsylvania High Plateaus. It even invades mature hemlock stands in increasing numbers where hemlock has failed to reproduce. This situation is reflected in the beech spectra above the hemlock maximum in Crystal Lake and Mud Lake. An increase in alder pollen in 6 spectra correlating the first beech decline and a slight dropping off of oak could indicate a local increase in the bog-shrub stage.

A warm-dry period ushered in the oak-hickory forest accompanied by marked increases in birch, maple, basswood, willow, elm and a slight increase in chestnut and ash. This forest resembles a typical oak-hickory forest of the type in the prairie peninsula of Indiana or that in the Low Hills belt of the Alleghany Plateau (Braun 1950). There is a pronounced increase in pollen of grass, sedge, ragweed, spatterdock, fern, and fern allies. Oak occurs in every spectrum of all the diagrams prepared in this study. Sears (1942) reports it has a considerable ecological range; he found it first in relative order of occurrence when compared to hemlock, hickory, beech, and basswood in 111 peat deposits throughout eastern United States, from Iowa to the Atlantic and from Tennessee to the St. Lawrence. These oak pollens must be from several species, although it is not possible to readily differentiate them microscopically in fossilized form. Oaks are among the top angiosperm pollen producers, and oak pollen may be windborne for great distances (Erdtman 1954).

The last climatic shift is to the moister-cooler climate of the present with oak, hickory, and beech diminishing, and pine and hemlock increasing in the Crystal Lake stratigraphy. Pine and hemlock are on the increase in the Mud Lake core and beech is decreasing, but oak is still high in numbers. The one spruce pollen grain at the surface spectrum in Mud Lake can be attributed to spruce plantations nearby, but the 13 spectra from the 8-1.5 ft, since they are low counts, could indicate wind-blown pollen from a considerable distance. This conflicts with the upper Crystal Lake stratigraphy in which spruce is absent. The surface spectra of Crystal Lake and Mud Lake reliably correlate the present vegetation of the Hartstown Bog area. Pine, hemlock, oak, alder, hop-hornbeam, ash, elm, beech, and hickory are in the surface samplings in the general proportions expected from the anlysis by line transect of nearby forest communities (Table I). Maple, tamarack, poplar, and willow pollen have a relatively rapid rate of decay if they are not embedded quickly in the sediments, and thus are found in low percentage, or not at all, in the surface stratum (Erdtman 1954).

Radiocarbon Dating

Two samples from the Crystal Lake sediments were analyzed by the C-14 radiocarbon dating method. Flint (1957) states that C-14 dating and correlation through palynological stratigraphy is the most reliable and accurate technique yet devised for recording the absolute chronology of the Pleistocene. One sample consisted of 5.0 g of fine peat from the 26.5 ft spectrum representing the pine maximum in the Crystal Lake pollen diagram. A second sample was composed of 1.563 g of wood fragments recovered from the 39 ft level. Although this quantity of material was far less than that ordinarily required for analysis, it was accepted for dating. The date on the peat was 9310 ± 150 yr B. P. (before present); that on the wood, which stratigraphically was 12.5 ft below the first sample, was 3265 ± 210 yr B. P. Two fragments of wood from the 39 ft spectrum were histologically examined. Both were identified as spruce (Brown and Panchin 1934).

Since there was sufficient material available in the peat sample for a good C-14 determination, the date of 9310 yr B. P. is assumed to be correct. It is then unlikely that there could be spruce in this deposit younger than about 8000 yr B. P. This consideration is based on the disappearance of spruce from the stratigraphy at the 24.5 ft spectrum. An alternative inference as to the origin of the spruce sample, assuming that it is correctly dated at 3265 yr B. P., would involve the occurrence of redeposition. The pollen analysis of the Crystal Lake core generally correlates with the normally accepted sequence for forest successions in northeastern United States (Sears 1930a, 1942; Deevey 1939; Potzger and Otto 1943; Krauss and Kent 1944; Potter 1947; Flint 1957) and renders the possibility of any redeposition here extremely remote. The carbon dating of this lower sample must therefore be considered erroneous.

Utilizing the 9300 yr B. P. as a point of extrapolation in time up and down the Crystal Lake diagram, some interesting correlations may be inferred. Assuming the deposition rate to be 173 yr for each 6 in. deposit, the 39 ft level would be about 13,500 yr B. P. Time of the maximum extent of the Cary substage in the Wisconsin glaciation (the substage dating the origin of the Hartstown Bog) is dated between 13,500 and

14,500 yr B. P. (Suess 1956). The Abies maximum at 32.5 ft would be about 11,000 yr B. P. and correlated with the Mankato substage or advance in the Wisconsin glaciation, which is dated as 11,000-10,000 yr B. P. (Suess 1956), and given as the date for the Two-Creek-Interval in Wisconsin by Flint and Deevey (1951). The minima in pine and spruce occurred during the maximum advance of the Mankato, whose terminal moraine has been identified about 80 miles north of the Hartstown Bog at Hamburg, New York (Flint 1947). If fir was at its maximum at Mankato time, then the climate in northwestern Pennsylvania could not have deteriorated to any crucial degree as a result of the Mankato advance, and the interstadial between Cary and Mankato as reflected in the spruce-fir of the pollen diagram was a cool-moist climate. The advance of the conifer forest northward following deglaciation may have been a steady migration into new areas, instead of a fluctuating back and forth in response to advancing and retreating ice sheets (Griggs 1934, Braun 1955). Every retreat and advance in glaciation cannot be interpreted from the maxima and minima of genera in the pollen diagram alone, nor are these successions in plant composition effects of the climate alone. Topography in relation to erosion and deposition, edaphic conditions, and biotic succession are other factors correlating the prevailing climatic type in the sequence of any forest region (Cain 1939).

Zumberge and Potzger (1956) correlate Lake Michigan Basin C-14 dates with pollen studies and place the oak-hemlock-broadleaf forest in the xerothermic, or hypsithermal (Flint 1957), period with a date of 4000 to 3500 yr B. P. In the Crystal Lake diagram the oak-hickory period can be estimated at about 3600 yr B. P. The 9310 yr B. P. determined C-14 date for the pine period at Hartstown Bog is in relative correlation with the 9000 yr recorded for the Cranberry Glades, West Virginia, which is on a latitude about 250 miles south of Hartstown, and over 200 miles south of the Wisconsin terminal moraine. Niering (1953) inferred the attainment of the pine maximum for a northern New Jersey bog, on a latitude 15 min south of the Hartstown Bog latitude, was about 8000 yr ago. The effect of topography on ice advance and recession may account for some difference in the date of the pine maximum in New Jersey on the eastern Pennsylvania border, and that C-14 date for the pine maximum in Crystal Lake on the western Pennsylvania border at the same latitude. Niering's New Jersey site is at an elevation of 1200 ft, and glacial striae are on the Kittatinny ridges in that area as high as 1800 ft. Although some of the Allegheny Plateau in northeast Warren County, Pennsylvania, where the terminal moraine enters the state, is 1900-2000 ft, most of the plateau averages between 1500-1700 ft, and was unglaciated. Deglaciation in these 2 areas at the 2 Pennsylvania border extremes could have proceeded at varying rates due to the differences in topography and probably in ice concentrations. Amelioration of climate might have set in earlier in northwestern Pennsylvania than in northeastern Pennsylvania and northern New Jersey.

The origin of these early coniferous forest bands mixed with oak, which so quickly migrated back into the glacial drift country, was suggested by Braun (1950) who stated, "The Unglaciated Allegheny Plateau and Allegheny Mountains doubtless served as refugia during the Pleistocene, and it is quite probable that at least a part of this area was continuously occupied during Wisconsin time by forest vegetation of a sort referable to the Hemlock-White Pine-Northern Hardwoods Forest." The apparent quick rate of forest species migration back into the Hartstown area upon deglaciation substantiates this theory. In view of the proximity of the area under study to the Allegheny High Plateau the consideration of such an invasion source is unequivocal.

There is, therefore, a need for evidence from deposits in the unglaciated region south of the terminal moraine in Pennsylvania to document the existence and nature of such a refugium which served as a source of plants for invasion into the barren drift county following recession of the ice.

SUMMARY

Three pollen profiles in the Hartstown Bog Area in northwestern Pennsylvania revealed a forest sequence with 5 major forest successions that suggest accompanying climatic changes. An initial spruce-fir forest with oak and pine as accessories is indicated, followed by a dominant pine forest with birch and oak understory, hemlock with co-dominant oak and accessory hickory and beech, dominant oak-hickory, and finally a forest with pines and hemlocks increasing, oak remaining, and beech and hickory diminishing.

Columbus Bog, 30 miles north of Hartstown, and Mercer Bog, 30 miles south of Hartstown, correlated with the bogs of the Hartstown area in the fir-spruce forest initial spectra.

The high percentage of oak, fir, and spruce in the earliest spectra rules out any long-sustained

or broad tundra zone inhabiting the glacial drifts subsequent to deglaciation in the Hartstown area.

Radiocarbon date determination for pine maximum from peat was 9310 ± 150 yr B. P. Extrapolating in both directions from the pine maximum, the relative ages in years of the various forests types are: beginning sediments, 13,000 yr; early pine and spruce minimum and fir maximum, 11,000 yr; and the oak-hickory spectra, 3600 yr. These dates and the general forest sequence correlate well with the composite northeastern United States and southeastern Canada pollen profiles.

The general absence of spruce and fir from the upper profile levels of the Hartstown deposits indicates a sustained amelioration of climate toward the establishment of a mesophytic environment in the areas contiguous to the terminal moraine.

Results suggest the need for study of deposits in unglaciated refugia in the area south of the Pennsylvania terminal moraine as well as on the Allegheny Plateau to determine the post glacial invasion sources.

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MUTUALISM BETWEEN THE MIDGE *CRICOTOPUS* AND THE ALGA *NOSTOC*[1]

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Introduction

Larvae of the dipterous family Tendipedidae are found in practically every aquatic habitat from the polar regions to the tropics. Some, of the genus *Spaniotoma*, live symbiotically with mayfly or stonefly nymphs, either under the wing-covers or clinging to the appendages (Johannsen 1937), whereas others live in freely movable cases of definite form, in fixed cases, or in mud (Edwards 1929). Many are leaf miners and may be restricted to a particular species of plant, either in terrestial plants (Needham *et al.* 1928) or in aquatic plants, such as cattails and reeds (Walshe 1951). A few members of the genus *Cricotopus* are known to invade the pondweed, *Pontamogeton* (Berg 1950).

The two species of *Cricotopus* considered in this paper have been studied in their relation to the colonial blue-green alga *Nostoc parmelioides.* Heretofore no investigation has been made of this relationship; the only recorded observation of the association was noted by Johannsen (1937). He mentioned finding small chironomid (tendipedid) larvae coiled in disks of the alga *Nostoc parmelioides* and ascribed them to the genus *Spaniotoma.* Adult midges reared for this project were sent to W. W. Wirth, at the National Museum, for identification. He noted two types present and described both as new species. He examined the material used by Johannsen and stated that they were indistinguishable from *Cricotopus.* Thienemann (1954) did not mention the midge or the alga in his classic work on fresh-water biology.

Nostoc parmelioides was first described in 1843, by Kützing. In his description there is no mention of a tendipedid larva. Forti (1907), Lemmermann (1910), Tilden (1910) and Geitler (1932) all described this species but did not mention the presence of an insect larva. Drouet (1939, 1942, 1943) referred to the species but wrote only of its distribution.

The filaments of *Nostoc parmelioides* are held together by a gelatinous matrix so that a flat, vertical thallus is formed, measuring about 12 mm in height and 1 mm in thickness (Figure 1). All *Nostoc* disks observed were found to contain a tendipedid larva or they showed signs that the larva had been present. The larvae are host-specific and have not been found in a free-living state.

The family name Tendipedidae is used throughout this study since it has priority over the better known name Chironomidae. The term "mutualism" as used in this paper means the living together of two organisms with benefit to both members.

This study was made at the University of California's Wildlife and Fisheries Experimental Station, at Sagehen Creek about 15 miles north of Truckee, California.

Methods

Monthly larval collections, made between September, 1954, and May, 1955, were all obtained from the same immediate area in Sagehen Creek; the scarcity of algal pads during other months necessitated collecting from a greater area of stream. The ratio of the 4th instar larvae to the number of pupae was obtained for each month in

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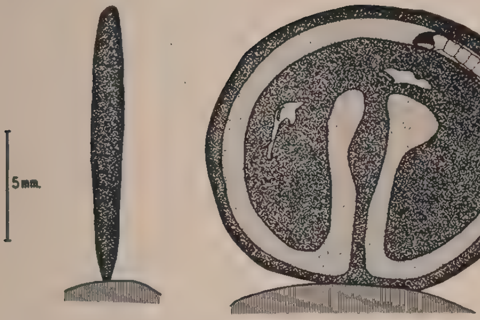

FIG. 1. Larval stage in the alga (end view and side view).

order to establish the major period of emergence for the tendipedid. Direct preservation of the algae in 10% formalin prevented the loss of pupae and larvae through emergence or through openings in the algae created during the process of collecting. This style of collecting gave a method for making comparisons among pads with larvae, pads with pupae, and pads that had been vacated.

The length of the pupal stage was determined by gathering 4th instar larvae that were ready to pupate and placing them in hatchery troughs which were fed by a flow of spring water. The dates of pupation and emergence were then noted. The swelling of the alga and the increased size of the tendipedid's thorax were signs that the time of transformation was near. The adults were captured and reared in small screen cages placed over the algal pads.

Determining the shape of the larval passageway

The excavation formed by the tendipedid always had the same characteristic shape. The older algal pads, being thin and transparent from the removal of matrix tissue by the feeding actions of the larvae, readily showed this passageway. Many of the younger pads were opaque, and if the passageway could not be seen by holding the pad in front of a light source, the algae were placed in a tightly closed jar, where they suffocated. With the death of the colony the algal pigments dissolved, leaving the blue pigment, phycocyanin, trapped throughout the tendipedid's tunnel and thus clearly showing the extent of the cavity.

Measurements of head capsules

Head widths were measured with an ocular micrometer. Measurements were made on the dorsal side of the capsules at their widest point near the posterior end. Capsule widths measured from newly hatched larvae verified the first instar peak. Occasional findings of cast skins from previous instars in the algal passageway with the larva helped to separate the stages. Shed capsules were not too reliable, however, since they were split in the act of molting, thereby losing their original shape. Immediately after a molt, the new head capsule was light in color and disproportionately large, so that a recently molted larva was easily recognized. The swollen thorax, characteristic of the late 4th instar stage, helped to identify this group as the last instar.

ALGAL LIFE CYCLE

Multiplication in the family Nostocaceae is either by means of specially differentiated resting spores called akinetes or by means of hormogonia (parts of trichomes). The cells divide within the spore forming a filament that later, after being released, develops into a colony. Hormogonia become separated from the trichomes when a weakening occurs in the chain of vegetative cells. The breakages occur most often at points where heterocysts (enlarged specialized cells) and vegetative cells join (Fritsch 1945). It is possible that the feeding activities of the tendipedid also create these breakages. After floating to a new location, the hormogonium comes to rest and grows directly into a new thread. The young colonies of *N. parmelioides* were spherical; those smaller than 2 mm did not contain tendipedid larvae. When the colonies reached a size of 3.5 mm or more, the larvae were usually present. At this size, the pads that were destined to stand erect became laterally flattened. Occurring less frequently was a 2nd form of *N. parmelioides,* the mature size of which was smaller than the vertical form. This was a horizontally flattened thallus with a verrucose surface, an irregular shape, and a swollen peripheral border wherein the tendipedid was always found. According to Chapman (1941), the form a colony takes will depend on the effect of the environment, which may determine the consistency of the mucilage. West and Fritsch (1927) state: "In no class have there been so many records of polymorphism as in the Cyanophyceae."

After the tendipedid had spent its larval stages within the alga and had pupated, the algal tissue surrounding the larva began to swell. The cortex was weakened and separated, creating an exit through the otherwise leathery algal sheath. The pupa forced its way through this exit and swam immediately to the surface of the water. Following the emergence of the tendipedid, the alga continued to decompose. All algae that were reobserved in the stream after the pupae emerged were completely disintegrated at the end of 2 weeks. Apparently, the death of the alga is caused by the removal of large amounts of algal tissue by the feeding of the larva, combined with the access of water through the break in the cortex. Experiments were tried to test the survival of the algae without the presence of the tendipedid, but the results were inconclusive because the methods of removing the larva usually injured the algal colony. However, during October, 1955, when many midge larvae were killed by an infestation of mermithid nematodes (see "predators"), the algal pads containing these dead larvae were yellow, thin, loosely attached to the rocks, and in a state of decomposition.

In Sagehen Creek *Nostoc* was most often found attached to rocks, which varied in size from pebbles (with just enough surface for the attachment of one algal pad) to large boulders densely covered with numerous pads. The alga was infrequently found attached to stationary sticks or branches in the water. At one location, where a hard clay bed prevailed, algal pads were found attached to the stream bottom. The depths at which the algae were found varied from directly below the surface, covered by only a small layer of flowing water, to the bottom of pools 3 feet deep. The algae were observed in both lentic and lotic waters, although there was a preference for the latter. *Nostoc* was frequently found growing on the elges of waterfalls and in the spillways. Colonies in swift running waters were frequently covered with simuliid larvae and pupae. There was no orientation of the alga to the direction of the current.

Development of the Insect Stages

Eggs

On April 24, 1955, a day after the emergence of 6 *Cricotopus* adults in captivity, 2 sticky egg masses were noticed in the water; one egg bunch was floating at the surface while the other was stuck to the bottom of the container. Two days after these adults emerged, a female was observed laying eggs, a process that took about 20 minutes. In the mass there were fewer than 100 orange, oval eggs. Their incubation period was not determined, since no males had been present and the eggs had not been fertilized. Fellton (1940) mentioned that female tendipedids emerging in the laboratory deposited eggs even though they had not mated. The incubation period for this subfamily is usually just a few days, according to Johannsen (1937).

Three egg bunches found attached to the upper edges of *Nostoc* pads on August 8, 1955, consisted of elongated gelatinous strings wound back and forth within an irregular mass. The largest of these groups had fewer than 500 eggs. Although these eggs were found in August, the breeding season is assumed to be in March and April, when the emergence period occurred. This cycle may fluctuate from year to year since the breeding season varies with weather and seasonal changes; there is a direct relation between water temperature and transformation (Sadler 1935). During March the maximum water temperatures at Sagehen Creek were between 36° and 46°F.

Larvae

The 2 species here concerned, *Cricotopus nostocicola* Wirth and *C. fuscatus* Wirth, can be separated from each other and from other species only in the adult stages. According to Wirth (1957), larvae of *Cricotopus* can be identified to groups only, the groups being based on larval structures and feeding habits. He recognizes 4 larval groups in this genus; the *Nostoc*-dwelling larvae belong to the 4th, previously unrecognized, group.

Cricotopus larvae were present in nearly all the algal pads examined, and there was never more than one mature larva per pad. Pads lacking a larva always showed the typical passageway that it had excavated at one time. Pupae were found at all times of the year, but the peak of emergence was in March and April. Therefore a large percentage of vacated pads was recorded in May (Figure 2). Observations of *Nostoc* in Sagehen Creek in 1955 indicated that algae were abundant from January through April, and scarce in July and August. This paucity of the alga is correlated with the tendipedid emergence period.

The typical tendipedid passageway found in every pad, and the position of the larva within the alga, are shown in Fig. 1. The tunnel followed the periphery of the pad until it reached the base and from there the 2 passages moved parallel to one another to the center. These 2 central passages were not connected at any point.

Larvae removed from the algae were very slow and awkward. The undulatory swimming motions usually characteristic of other tendipedids were entirely lacking. They showed no ability to wriggle or to crawl when out of their algal passageway. In the passageway, however, the tendipedid moved very rapidly. When the larva moved forward it would seize the tissue of the alga with its mandibles and arch the thorax over its head. When

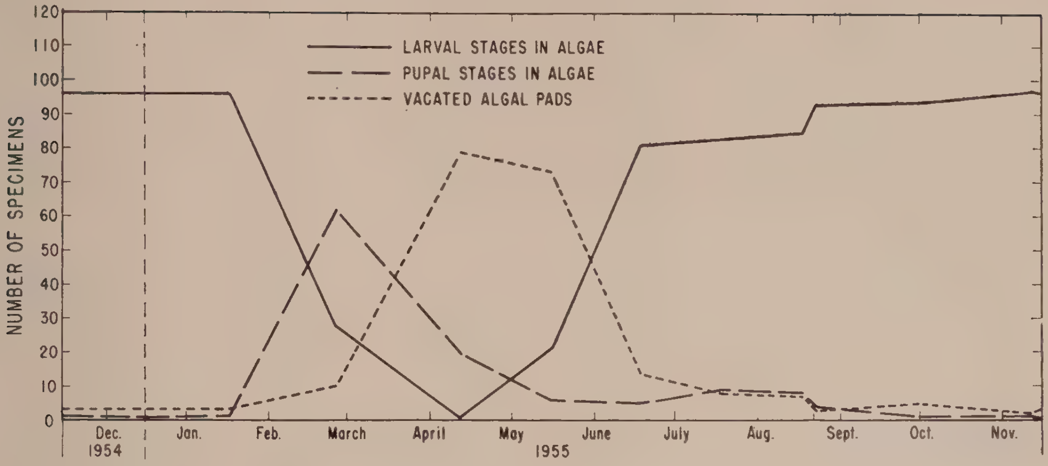

FIG. 2. Seasonal abundance of larvae and pupae.

the mandibles were released the anterior prolegs would seize the alga. The head would then be pointed forward and the mandibles would again grasp the alga. When the larva reached the end of the passageway it would reverse its position by sharply turning on itself in order to start off again with the anterior end forward.

In addition to the one large larva present in every mature algal pad, there could also be found several earlier instar *Cricotopus* larvae. These small larvae were distributed throughout the pad, where they created their own tunnels by eating their way through the alga (Fig. 1). Algae with one small larva were most abundant; pads with more than 10 larvae were less frequent. An algal colony sometimes included 50 larvae or more. In such a situation it was suspected that an egg mass may have been deposited on the algal pad and that the larvae, after hatching, had entered the nearest available plant. Berg (1950) noted similar occurrences in *Cricotopus elegans,* which mines in the aquatic *Potamogeton*. He said (p. 89): "Since all young larvae present in a group of several leaves floating together usually are concentrated in only one or two of the leaves, it seems likely that eggs are deposited in masses on or near *Potamogeton* leaves, and that newly hatched larvae tend to enter the nearest, most desirable, or most accessible leaf, and roam for short distances in search of fresh food as they grow older." He found that there was no restriction on the number of mature larvae of *C. elegans* per leaf, but that there was a limit on the number of penultimate-stage larvae—no more than 3 per leaf. More than 20 first instar larvae, in contrast, might riddle a leaf with an irregular network of criss-crossing mines.

There are several possibilities by which *Cricotopus* may invade the algal pads within a given locality. When an egg mass is deposited on an alga, the larvae that hatch will invade that pad. Larvae, on emerging from the egg mass, might be distributed by being swept downstream. It was noticed that, when small buds formed at the base of older algal colonies, they were occupied by young larvae. If these buds should separate from the parent plant, they would then already contain a tendipedid. Also, as Berg (*op. cit.*) mentioned, when the tendipedids grow older they start to roam in search of food. Young larvae removed from their algal pads and placed in a container along with available pads soon re-entered them. The larva entered the alga anywhere on its surface, by eating a hole into the cortex and channeling through the matrix.

In addition to being found in the large *Nostoc* pads, the first 3 instars were observed as solitary individuals in very small algal colonies. In small pads up to 3.5 mm in height, the tendipedids formed a semi-circular passageway following the contour of the pad. When the plants were about 4 mm in diameter the ends of the tunnels were extending up from the base toward the center.

While living within the alga, the tendipedid fed exclusively on the algal matrix; *Nostoc* filaments were abundant in the stomachs of the larvae. Many other aquatic species of tendipedids living as leaf miners produce currents through their burrows by dorsoventral undulations of their bodies, thus securing plankton. *Cricotopus,* however, had no exit holes along any part of the pathway. Larvae that were placed in glass tubing of the same diameter as the algal passageway showed no undulatory movements nor revealed any attempts to construct nets or webs. A mining larva subsisting on the tissue of the plant that shelters it must extend its excavation as it feeds or abandon it and make a new excavation. Fourth instar *Cricotopus* larvae apparently never moved from pad to pad in search of food. After the mines were extended to a certain point, the larvae would start to increase the diameter of the tunnel. Doubtless, some algal tissue was regenerated. *Cricotopus fuscatus* and *C. nostocicola* larvae are assumed to host-specific since they have not been found in a free-living state or in any plants other than *Nostoc parmelioides.*

No traces of excrement were found in the tendipedid's passageway. Needham *et al.* (1928) mentioned terrestrial leaf miners that eject all their frass through a hole in the epidermis of the leaf. They state that there are other leaf miners (certain Lepidoptera and Diptera larvae) that have their mines almost filled with frass pellets, resulting in a "very messy appearance." On one occasion a larva that had been removed from the alga was observed to eject a small amount of yellow fluid. Since no fecal material was found inside, and exits from the passageway were lacking, it is probable that the waste material consists of this yellow fluid, which diffuses between the filaments after it is ejected.

According to Leathers (1922), the larval stages of the Tendipedidae extend over a period varying from 25 to 30 days to all winter, depending on food and weather.

From the insects collected at Sagehen Creek it was established that there were 2 species, both of them new (Wirth 1957). The adults of the 2 species (*Cricotopus nostocicola* and *C. fuscatus*) are dissimilar in appearance, but their larvae do not have any obvious characters whereby they may be separated.

Johannsen (1937) described certain species of the subfamilies of Tendipedidae, and in one description mentioned finding a small larva coiled in the disk of the alga *Nostoc parmelioides.* This larva was designated by him as *Spaniotoma* sp. G. In comparing 2 of Johannsen's larval slides of specimens from Cos Cob, Connecticut, and one larval slide from *Nostoc* in the Callowash River, Oregon, Dr. Wirth concluded that the specimens determined by Johannsen as *Spaniotoma* sp. G were indistinguishable from the larvae of *C. nostocicola* and *C. fuscatus.*

Head capsule measurements are used as a basis for determining the number of instars since they remain fairly constant while within the instar, but increase in size, with each succeeding molt. In all, 360 head capsules were measured. The 4 different peaks in Figure 3 indicate the modes of 4 different head capsule sizes. The range of variation for the 4 instars is 0.01 mm, 0.05 mm, 0.10 mm, and 0.11 mm, respectively.

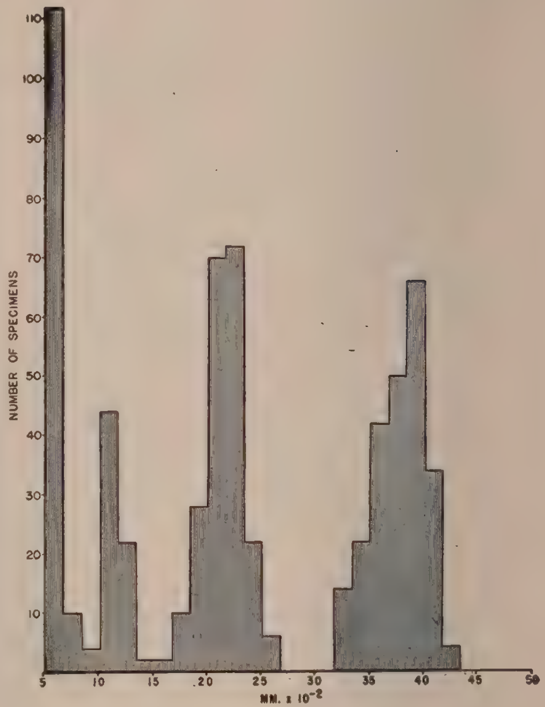

FIG. 3. Distribution of larvae according to widths of head capsules.

First instar

The head capsule of the newly hatched larvae were disproportionately large; the head width at that time measured 0.07 mm. The first column in Fig. 3 represents the width of the head capsule immediately after hatching. The head capsule widths measured 0.07 mm to 0.08 mm. The mean head width was 0.071 mm. The body of the larvae of this instar had a violet pigmentation and the digestive tract had a visible yellow coloration. The head capsule was dark brown. The average length of the larvae was 0.5 mm. This stage was found in the randomly built passageways within the large *Nostoc* pads and also in the very small algal nodules.

Second instar

The head capsule widths measured from 0.10 mm to 0.15 mm. The mean was 0.12 mm. The abdomen was a light violet, in contrast to the darker violet pigmentation of the thorax. The yellow coloration of the digestive tract was still visible. The head capsule was black. The body lengths ranged from 1.00 mm to 1.50 mm. Larvae of this instar were found in small *Nostoc* pads as solitary individuals or in large algal pads, where they occupied the small random passageways.

Third instar

The head capsule widths ranged from 0.17 mm to 0.27 mm. The mean was 0.22 mm. In this instar the violet pigmentation was retained by the thorax whereas the abdominal coloration was replaced by a bright yellow. The head capsule was black. The body lengths ranged from 1.00 mm to 2.75 mm. Larvae of this stage were found as solitary individuals in small algal colonies or in large pads, where they were not in the main peripheral passageway. This instar, as well as the 4th instar, was occasionally infected with a nematode.

Fourth instar

During the 4th larval stage the head width and body length increased greatly. Head widths ranged from 0.32 mm to 0.43 mm with a mean of 0.38 mm. Body lengths ranged from 3.50 mm to a maximum larval length of 8.25 mm. The head capsule was black and the entire body was a bright yellow. This instar always inhabited the peripheral passageway of the alga. Just before pupation the thorax would become greatly enlarged (Figure 4), signifying that transformation was about to take place. Simultaneously the larva would excavate a small cavity in the alga, which later served as the exit pathway for the pupa. This short path was always excavated only to the cortex of the alga, and never through that layer. At the same time a change would take place in the shape and structure of the alga. The entire area surrounding the larva would swell (side view, Fig. 4) and continue to swell until the cortex was weakened and broken, allowing some of the softer inner parenchyma tissue to protrude (Figure 5). This break in the outer layer provided an exit for the pupa.

Pupal Stage

The length of the pupae ranged from 4.50 mm to 7.25 mm. The color varied from a bright yellow to a deep orange. The orange was characteristic of a female containing eggs in the abdomen. Many of the pupae had the abdomen contracted within the pupal skin, leaving the last few segments empty.

A very much enlarged upper portion of a *Nostoc* pad indicated the presence of a tendipedid pupal stage (Fig. 5). The entire pupal period was spent within the alga. This period varied from 5 to 9 days, with a mean of 6.7 days. When the pupa was mature and ready for its final molt, it left the alga. This action was probably similar to the behavior of miners in *Potamogeton* (Berg 1950) which created vertical undulations of their bodies until they were able to break through the plant tissue. After leaving the alga, the pupa presumably swam to the surface of the water, where the pupal skin was split along the dorsum of the thorax, allowing the adult to emerge. The pupal exuviae floated freely on the water; those of the last larval instar remained in the passageway.

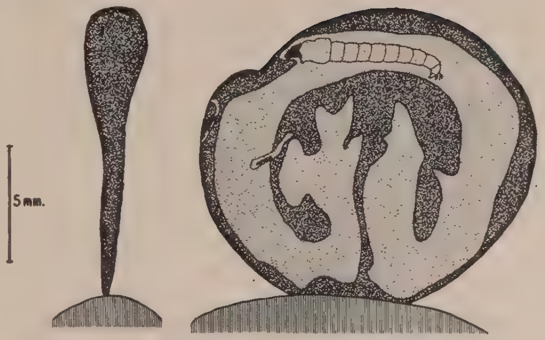

FIG. 4. Late larval stage in the alga (end view and side view).

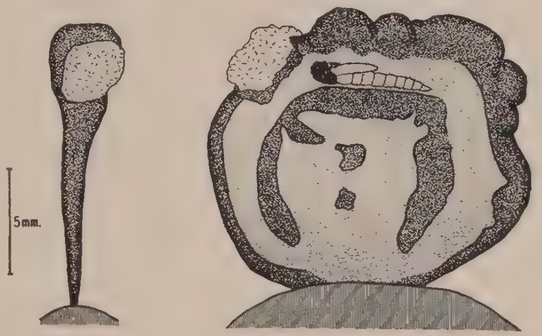

FIG. 5. Pupal stage in the alga (end view and side view).

Adult Midges

Wirth (1957) stated: "Although adults of the two species do not have the prominent white-banded legs, pale-banded abdomen, or whitish genitalia characteristic of *Cricotopus* in the strict sense, the presence of dense pubescence on the eyes, absence of macrotrichia on the wing, absence of distinct erect hairs arising from obvious punctures on the mesonotum, and presence of a complete fringe of hairs on the squama place both species in *Cricotopus,* Group C of Edwards (1929). . . ." The fact that most of the adults that were reared lived only one day after emergence was probably due to their confinement. According to Leathers (1922), the longevity of the adult stage of tendipedids is brief but lasts 5 to 10 days.

Predators of the Tendipedid

Tendipedids constitute an important food item in the diet of many predacious animals. In the larval and pupal stages they are devoured by aquatic beetle larvae, waterbugs, the nymphs of dragonflies, damselflies, and stoneflies and by caddisworms, salamanders, and fish (Leathers 1922). Ping (1917) observed that the larvae of tendipedids were preyed upon by the copepod crustacean *Cyclops* and that the adults were preyed upon by bats, which were seen to fly across the swarms. Fish may be predacious on *Cricotopus,* but other dipterous larvae and parasitic nematodes are known to be the main predators.

Other Tendipedids

A 2nd type of tendipedid with a life cycle that may be very similar to that of the *Cricotopus* species was occasionally found in the *Nostoc* pads. This tendipedid also belonged to the subfamily Hydrobaeninae but had a much larger, less tapering, brown head, with longer hairs on the body. Most often they were found in their own passageways, which were distributed at random in the same fashion as those of young instars of *Cricotopus,* but occasionally they were observed in the large passageway. When this situation prevailed, the dead body of a *Cricotopus* larva or pupa was also present in the channel. It is therefore assumed that this tendipedid may be predatory on *Cricotopus,* though this could not be established in the laboratory by placing the 2 larvae, free of the alga, in a common container.

The 2 larvae appeared superficially similar but were easily separated by their behavior. *Cricotopus* moved very slowly when out of the alga, whereas the other tendipedid was very active and had the ability to wriggle. When they were examined more closely, the 2nd type was distinguished by its much longer anal hair tuft, longer and less tapering head capsule, more clearly separated body segments, and a slightly darker coloration; the mature larval size of the 2nd tendipedid was much smaller.

On August 12, 1955, five gelatinous egg masses found attached to *Nostoc* colonies were brought into the laboratory. Five days later, when all the young larvae had emerged, it was noted that 2 types of tendipedids were present. One type showed a very active wriggling motion, a very long anal bristle, a transparent white body, and reddish eyes. *Cricotopus* could be told by its slow, awkward motions, much shorter anal bristles, violet and yellow body coloration, and black eyes and head capsule. The life cycle of the 2nd tendipedid may be similar to that of *Cricotopus,* since its egg masses have been found attached to the upper edges of the *Nostoc* pads and its larvae have been found eating their own pathways through the algae; it is also known to pupate within the alga.

Cranefly Larvae

Cranefly larvae of the genus *Antocha* were often noticed in collections of algae brought into the laboratory. These larvae were most frequently associated with the horizontal form of *Nostoc,* where they were found inhabiting the area under the alga. Since it is known that tipulid larvae are predatory on small aquatic organisms, there is a possibility that they may be predators of *Cricotopus.* Only in one instance was an *Antocha* larva found inside the tendipedid passageway; no midge larva was present. Once again, no evidence of predation could be established by placing the 2 types of larvae together in a container.

Parasitic Nematodes

In reference to leaf miners and parasites, Needham *et al.* (1928) state: "In the beginning, the mine may have been a place of comparative security from parasites, but it is not so now. Once the parasite has learned how to effect an entrance, the miner is worse off than its free-living ancestor, having no means of escape. A very high percentage of parasitism is the rule among leaf-miners."

Of the predators found, the one that was responsible for the highest mortality was a roundworm belonging to the family Mermithidae, a group common as insect parasites. Certain tendipedid larvae collected during the course of the year were light green instead of bright yellow; this green was due to the presence of the mermithid parasite. Some of the midge larvae were just as active as the uninfected larvae, whereas in others the presence of the roundworm had slowed their activities so that the only movement present was that caused by the writhing of the nematode within. The latter condition probably meant that the nematode had undergone its last molt and was now ready to leave the tendipedid. The length of the nematode was usually 3 or 4 times that of the midge larva. This excessive length meant that

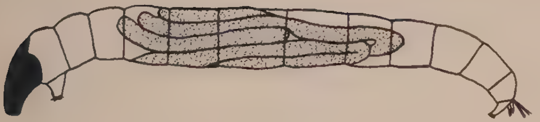

FIG. 6. Parasitic nematode within the midge larva.

the roundworm was curled back and forth within the larva occupying nearly the entire body cavity (Figure 6). The digestive tract of the tendipedid was pushed to one side, against the body wall.

The nematodes were found in the 3rd and 4th instar larvae as well as in the pupae. In August and September of 1955 they were present in small numbers, but in October of that year they had become very abundant. In a random sample of 100 larvae, 9 were infected. Those algal pads containing infected or dead larvae were very thin and yellow toward the base and loosely attached to the rocks. The dead tendipedids were no more than the larval skins that the nematode had left behind when it escaped. Infected larvae were removed from the algal pads and placed in a separate container. After the roundworm had escaped from the larvae, they were removed and placed in a container of mud and water, where they were allowed to mature. These roundworms were removed one month later and preserved for identification.

According to Filipjev and Stekhoven (1941), the adult mermithids are free-living and occur either in aquatic habitats or in the soil. They state that the host dies either from exhaustion caused by the food consumption of the parasite or by secondary bacterial wound infection.

Christie (1942) and Hyman (1951) both gave accounts of a mermithid found within a tendipedid larva. The life cycle of *Paramermis contorta,* a nematode found in a *Chironomus* sp., is probably very similar to the life cycle of the nematode in *Cricotopus.* The host can become infected either by eating the mermithid eggs or through being penetrated by the juvenile worms. The young nematode can better penetrate a larva that has recently molted and has a soft cuticle. With *Cricotopus,* the nematode possibly has a method of entrance into the alga before it penetrates the tendipedid. All infected *Cricotopus* larvae had only one roundworm present. Christie and Hyman go on to state that the nematode dwells in the haemocoel, where it is very destructive to the viscera and body fat, killing the host or rendering it incapable of metamorphosis or reproduction. After the parasite has spent its juvenile stages in its invertebrate host it leaves and does not feed in the adult stage. The parasite may exit through the anus or force its way directly through the body wall, the majority emerging just before their insect host would normally pupate.

Fish

Tendipedid larvae and pupae constitute one of the staple food items in the diet of nearly all carnivorous young fish. They are used as food for young fish in hatcheries, and the use of *Chironomus tentans* was recommended by Sadler (1935) in a publication in which he described special methods for its propagation. One can therefore understand why the habitat occupied by *Cricotopus* is beneficial to the species, although it is likely that *Nostoc parmeliodes* may be taken occasionally. Hildebrand and Towers (1927) surveyed the food of trout in Fish Lake, Utah, and reported that "rounded egg like masses of dark green *Nostoc* colonies are common on gravelly shallows, and are not uncommon in fish stomachs." They further stated that investigation of the ingested material indicated that the globular colonies of *Nostoc* were fed on rather regularly. They observed that there was a considerable variation in the size of the colonies taken but that the average diameter was about 4 millimeters. Dr. Richard Gard, working at Sagehen Creek, informed me that he found no *Nostoc* pads in examinations of more than 100 stomachs from rainbow, eastern brook and brown trout taken at all times of the year. The only time that *Cricotopus* would be directly available as food for fish would be in its adult stage, when it flies near the water, especially during oviposition, or during its emergence period, when the pupa leaves the alga and swims to the surface of the stream.

TENDIPEDID'S ABILITY TO ERECT THE ALGAL PAD

When algal pads were torn from their original holdfast, the tendipedid had the ability to erect them to an upright position and refasten them to the substrate. If the alga was so large that the larva was unable to place it upright, the pad would be fastened in a horizontal position. This process was observed under artificial conditions when the pads were torn from the rocks and placed in hatchery troughs. During the spring snow melt, when freshets cause the rolling of rocks and the scouring of the stream bottom by debris, there is a noticeable lack of *Nostoc* in Sagehen Creek. It may be at this time of the year that the larvae benefit the alga by reattaching the pads to the stream bottom.

Algae were gathered from the stream and brought into the laboratory for observation of the reattachment procedure. Removal of the alga from the rock usually created a break near the base of the pad. If these algal disks were placed in a dish of water and left undisturbed, the tendipedid would protrude its head and thorax through the hole in the pad. If the container was jolted in the slightest way, the larva would retract itself and not come out again until the water had settled. While raising the algal pad to a vertical position, the tendipedid never left the pad; instead, it projected the anterior half of its body from the pad and sought a secure hold with its mandibles. When the hold was established, it pulled the pad over to the point. While the larva held fast to the substrate, it started to erect the pad. During the struggle to gain control of the alga, the larva caused the pad to sway back and forth. When the alga was vertical and under control, the tendipedid cemented the edges of the torn area to the substrate. In a few minutes the pad was so secure that it could be probed with a needle without being broken loose.

Some of the larger pads, and a few of the smaller ones, were raised only to a 45° angle or not raised at all; in the latter instance they were cemented to the substrate in a horizontal position. The larva would usually create a hole at 2 different locations and cement the edges to the substrate. On many occasions when quantities of *Nostoc* were collected and placed in one container, the algae were fastened to one another by the action of the larvae. In one experiment, 34 pads were placed in an enamel pan and only 2 failed to become reattached. Of the 2 pads that were not attached, one had been vacated by the larva.

Distribution of the Alga and Insect

The distribution of the alga was established from personal observations, from specimens of the alga in the University of California Herbarium, and from the literature. Most of the herbarium specimens of *Nostoc parmelioides* that were examined readily showed the typical tendipedid passageway and the larva. If the features were not immediately noticed, because of opaqueness caused by the blue and green pigments, the alga was held up to a light source to help reveal the channel and the tendipedid. In other pads the presence of the larva could be detected by the prominence of the head capsule. When the algal pads had been dried on paper, the plant tissues as well as the body of the larva had contracted but the head capsule retained its shape, forming a readily noticeable protrusion in the algal pad.

The alga and its associated larva are found throughout California, but most of the records are from the cold streams of the high mountains in the Sierra. Outside of California there are scattered records of the alga in many states, all the way to Connecticut. It was not established whether the tendipedids were present in the *Nostoc* reported to occur outside the United States. The material that Kützing used for his original description was collected from a mountain stream in the Thuringian Forest, near Suhl, Germany. Thienemann (1954) did not mention the midge or the alga as occurring in Europe. Geitler (1932) described the alga and stated that its distribution was Europe, the Antilles, North America and Africa. In none of these accounts was the presence of a tendipedid mentioned. Among the specimens of algae examined in the herbarium there was one collection from the Kropbach River, a tributary of the Dos River near Geroldsau, Baden, Germany. These pads were too small to detect the presence of a tendipedid.

Advantages of the Interrelationship

The advantages of this symbiotic association are more obvious for the tendipedid than for the alga. The tendipedid, living within the alga, receives shelter and protection from adverse conditions. It is partially protected from fish and predatory insects. It has a constant food supply since it feeds on the alga. When the stream level drops, the alga may be an insurance against the immediate desiccation of the tendipedid, since algal pads were observed above the water level with larvae still alive inside. The alga may thus help keep the larva moist until the stream level rises again.

The main advantage of the relationship to the alga is found in the ability of the larva to reattach the colony to a firm substrate. If it were not for the midge larva the pad would continue to drift downstream. By erecting the *Nostoc* pad to a vertical position, the larva may help to expose the alga to a greater amount of sunlight. By its feeding activities upon the trichomes, the larva helps to create more reproductive filaments. Smith (1933) mentioned that hormogonia are formed by breakage of trichomes, and that "breaking may result from animals feeding on the filament. . . ." He also stated, in reference to *Nostoc,* that "the large number of trichomes within the adult colony is largely the result of development of these hormogones into new trichomes without their being liberated from the colonial sheath." Thus, when the tendipedid pupates, its influence in breaking the algal cortex may be an aid to the release of hormogonia. Although the parent colony is destroyed, many potential new colonies are liberated.

Since both the tendipedid and the alga apparently benefit from the intimate symbiotic association, the more specific designation "mutualism" may appropriately be applied to it.

SUMMARY

Midge larvae living in the blue-green alga *Nostoc parmelioides* Kützing (1843) taken from Sagehen Creek, Nevada County, California, were reared and found to represent 2 new species. The tendipedids, *Cricotopus nostocicola* Wirth (1957) and *C. fuscatus* Wirth (1957), can be separated only in the adult stage since no characters were found to distinguish the larvae. Measurements of head capsule widths of the mixed populations revealed the presence of 4 larval instars, each with a distinctive color pattern. There was never more than one last instar larva in an algal pad. Every algal pad examined contained the larva or showed the characteristic passageway created by the larva in feeding. Younger instar larvae were also found in the larger pads, but their passageways were irregular in shape and distributed at random. Pupation always took place within the alga; pupae were found during all seasons of the year but the peak of emergence occurred in March and April. Just before pupation, the larva created a small excavation toward the cortex. This channel was later used by the pupa as an escape exit. Simultaneously the algal tissue surrounding the larva began to swell and enlarge, until the leathery surface layer of the alga was weakened and broken. When the pupa was ready to leave the pad, it pushed its way through this area of weakened tissue, swam to the surface, and emerged. After the tendipedid had departed, the alga continued to decompose.

Although such a niche is of protective value to the tendipedid larva, it by no means offers complete safety, since a parasitic nematode played an important role in larval mortality. For the tendipedid the main advantages are shelter, food, and protection from most enemies. *Nostoc* gains from the relationship because the larva is able to cement the alga to a firm substratum whenever it is dislodged. The tendipedid's presence may also enhance the reproductive methods of the alga. Hence, the relationship of the midge and the alga has mutual advantages—a case of mutualism.

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WILLOW AND ASPEN IN THE ECOLOGY OF BEAVER ON SAGEHEN CREEK, CALIFORNIA

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Introduction

Like many other mammals, beavers thrive in sub-climax vegetation. Specifically, they often flourish where fire has been followed by appearance of Quaking Aspen, *Populus tremuloides*. This tree is the one most commonly felled for food and building material by beaver and its distribution is remarkably similar to that of the beaver.

Where beavers do occur in the absence of aspen, they usually depend on willow. Various species of *Salix* are found even more widely distributed than aspen, and very few beavers maintain themselves outside its range although they may temporarily subsist on such unlikely forage as sagebrush or cornstalks. As a matter of fact willow is often abundant in conjunction with aspen, and West and Rasmussen (1947) feel that willow, not aspen, is the key plant in beaver habitat.

The primary purpose of this study has been to analyze and interpret patterns of use of varying supplies of willow and aspen at 3 beaver colonies in the northern Sierra Nevada.

Several investigations similar to the present one have been most helpful and interesting for purposes of comparison. Notable are those of Aldous (1938) in Minnesota, Bradt (1938) in Michigan, Gese and Shadle (1943) and Tevis (1950) in New York, Haas (1943) in Utah, Haseltine (1948) and Hodgdon and Hunt (1953) in Maine, and MacDonald (1956) in Colorado.

The Study Area and its Vegetation

Sagehen Creek, about 8 miles north of Truckee in Nevada County, drains a basin approximately 12 miles long on the east flank of the Sierra Nevada. The stream empties into the Little Truckee River. Along its easterly course it drops from an elevation of 8000 to 5800 feet.

Quaking Aspen, *Populus tremuloides,* and 4 species of willow—*Salix cordata, S. glauca,* var. *villosa, S. Lemmonnii* and *S. argophylla*—constitute the principal forage species for beavers. The willows are found in wet sites or along the border of the stream for almost its entire length. Aspen occurs where the soil is relatively moist, but it is less restricted to the immediate vicinity of the stream than are willows. The distribution of aspen along the length of the creek is decidedly spotty.

Aspen stands typically spring up in the wake of forest fires. Most of the Sagehen basin has been lumbered and burned over. Mr. Charles B. White, a retired Truckee banker, recalls that much lumbering was going on in this area when he arrived in 1896, and it continued until about 1910. More than half of the 25 aspen trees aged by core-samples took root during the 1910-1928 period; the rest were established randomly from 1840 to 1890. This suggests that much of the present stand of aspen had its origin in fires immediately following the lumbering operations recalled by Mr. White.

Woody plants known to be cut by beaver on Sagehen Creek are:

Quaking Aspen	heavily
Willows	heavily
Mountain Alder	fairly heavily
Ceanothus velutinus	very lightly
Currant	lightly
Lodgepole Pine	very lightly
White Fir	lightly
Grasses	unknown extent

Although aspen and willow were the most important items cut by beaver, almost every woody plant was cut to some extent. White fir was often felled and was always barked in a characteristic way. Whereas the bark of the stump and lower trunk of felled aspen was almost always ignored in favor of the bark and twigs of the smaller terminal branches, the opposite procedure was followed with fir. There is apparently some ingredient present in bark or sap of the basal part of firs which is sought.

Mountain Alder, *Alnus tenuifolia,* especially in the upper reaches of the creek, is a conspicuous streamside plant and is used to some degree by beaver. Lodgepole Pine, *Pinus contorta,* is another conspicuous tree which is restricted to the vicinity of the stream and is often killed by flooding of the beaver ponds. Both the Jeffrey Pine, *Pinus jeffreyi,* and Ponderosa pine, *P. ponderosa,* are abundant on the upland slopes, the former occurring mostly above 6300 feet elevation.

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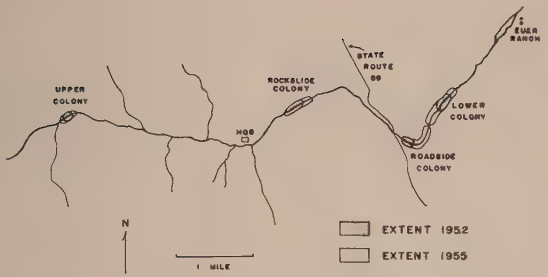

Fig. 1. Expansion of beaver colonies on Sagehen Creek, 1952-1955.

On the very highest slopes at the head of the basin and on one steep, cool north-facing slope farther downstream are stands of Western White Pine, *Pinus monticola.* White Fir, *Abies concolor,* Red Fir, *A. magnifica,* Mountain Hemlock, *Tsuga mertensiana,* and Sierra Juniper, *Juniperus sierrae,* complete the list of evergreens.

Ceanothus velutinus forms extensive stands of almost impenetrable chaparral on the burned over and logged over slopes at the head of the basin, and farther down the watershed on the south-facing exposures where it is mixed occasionally with Manzanita (*Arctostaphylos* sp.).

Bitterbrush, *Purshia tridentata,* and Sagebrush, *Artemisia tridentata,* particularly the latter, cover flatter, drier sites, forming unbroken stands in the lower reaches of the watershed.

Description of Colonies Studied

Figure 1 shows the locations and extent of 4 of the beaver colonies, 3 of which were studied in detail. For the purposes of this study, Bradt's (1938) definition of a colony was used: ". . . a group of beavers occupying a pond or stretch of stream in common, utilizing a common food supply, and maintaining a common dam or dams. They may or may not be living in the same lodge or burrows."

As shown in Figure 1, all the colonies expanded during the period of study. Only the Rockslide colony vacated any of the original colony site.

Figure 2 presents detailed maps of the 3 colonies and shows the extent of aspen, location of my sampling areas, and various beaver-made features such as dams, lodges and ponds. Owing to the nature of willow growth it was not practical to map its extent in the various colonies; it grew in clumps along the shores and on almost every little island, spit or exposed shoulder on the dams. Willow growth extends, roughly, from shore to shore the length of each colony.

The supplies of willow and aspen were highly variable from colony to colony. The Upper colony had abundant aspen but very little willow; the Rockslide colony had almost no aspen and an intermediate supply of willow; and the Lower colony had an intermediate supply of aspen and a great deal of willow.

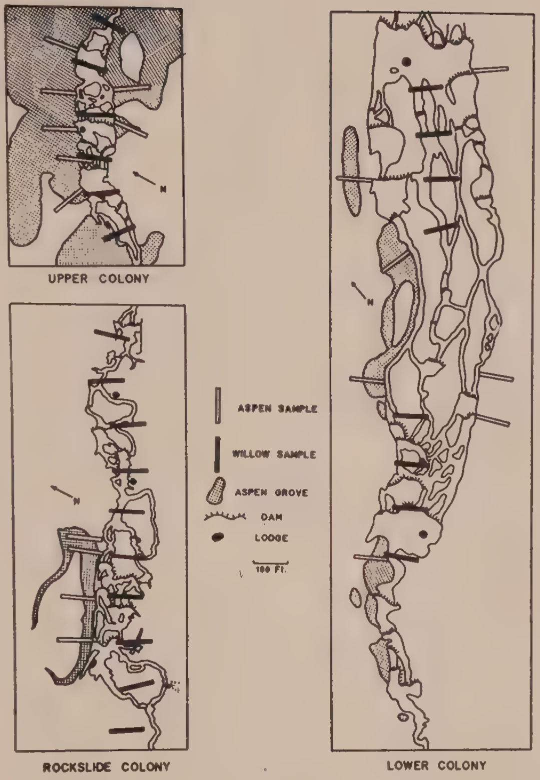

Fig. 2. Extent of aspen and location of sample plots on the three colonies studied.

Population Size, Activity and Behavior

For the results of the willow and aspen measurements to be most meaningful a census of each colony was necessary. Knowing the number of animals per colony during a given season permits one to calculate forage use on a beaver-day basis and thus make comparisons between the colonies. A census of each colony was made by applying the Lincoln Index method to the ratio of marked to unmarked animals seen during evenings of observation.

Trapping and Marking

Four Bailey live-traps, the type widely used by the state trappers in the West and recommended by Bradt (1938), Grasse and Putnam (1950), and Hodgdon and Hunt (1953), were used in the summers of 1953, 1954, and 1955.

In the past most field workers have had good success ear-tagging beaver with monel metal, fingerling type fish tags, (Harris and Aldous 1946, Haseltine 1950, Rasmussen and West 1943). However, an obvious field mark was needed for the purposes of this study. Such a mark would permit an observer to obtain a Lincoln Index ratio on the basis of sight records rather than the less efficient method of re-trapping. In addition, activity and behavioral differences, if any, could be observed among individuals in a colony. The method finally adopted was notching the tail by means of a large-size pig ear-notcher. No more than 2 notches per animal were necessary. Beavers showed little or no reaction or bleeding and the marks have remained easily visible, in one case for 5 years. Recently David Taylor, studying these same colonies, has had good success marking beavers on the tail with waterproof spray enamel. These marks last at least a month and are much more easily recognized at a distance than are tail notches. In some cases scars and other natural marks on the dorsal surface of the tail were found to be reliable field marks.

Sexing the animals was accomplished by external palpation for the penis bone as described by Rasmussen and West (1943), and as demonstrated by Clyde J. Shehorn, state beaver trapper for the California Department of Fish and Game. The method of palpating the testes, described by Osborn, (1955) was tried several times during the 1955 season with indifferent success, probably because of inexperience on my part.

Population Estimates

In the 1954 season 5 individuals were trapped at the Upper colony. The breeding female and one kit were found in the traps dead of exposure, and another kit, although released alive, was in very poor condition at the time and was thought to have succumbed shortly after its release. An adult, probably the breeding male, and a yearling female were trapped, marked and released without injury. A 6th beaver, probably a yearling, was never taken in the traps but was occasionally observed. The colony is thought to have consisted of a pair of breeding adults, 2 yearlings and 2 kits at the start of the 1954 season. Following the trapping losses, 2 yearlings and the adult male remained.

Evidently the loss of the breeding female was a serious blow to the colony, for in 1955 only 3 animals were observed. They were the adult male and the animal taken as a yearling in 1954 plus an unmarked individual thought to be the same unmarked beaver seen in 1954. No kits were seen here in 1955, presumably because the 2-year old female was not in breeding condition. Osborn (1953) found that only about 20% of the 2-year olds examined by him had bred.

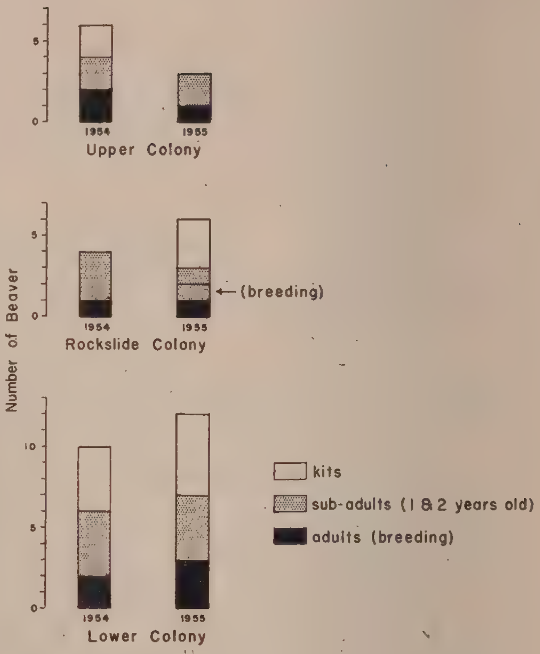

FIG. 3. Beaver population estimates for 1954 and 1955.

At the Rockslide colony the adult female also was killed in the trap in 1953. The subsequent population of this colony in 1954 was 4 animals, including an adult male and 3 smaller beaver, but no kits. It is significant that here, as at the Upper colony, no kits were seen in the season following one in which an adult female was killed, indicating that none of the 2-year old females had replaced its mother as a breeding female. In 1955 reproductive activity resumed and the population rose to 6, including the breeding male marked the previous season, a lactating female, another animal about the same size as the lactating female and three kits.

The only year in which beaver were trapped and marked at the Lower colony was 1955. In that year the population was thought to consist of 12 animals. An estimate of 10 beaver, based only on observations of unmarked individuals, was made for the previous year.

Figure 3 summarizes population estimates for the 3 colonies.

ASPEN

In this phase of the study the problem was 2-fold: 1) to measure the available amounts of aspen, of assorted sizes, and 2) to measure the rate at which the beaver were cutting the trees.

Methods

A sampling method was employed for calculation of availability of the different diameter classes of aspen trees, in terms of density per unit area. After the extent of aspen cover had been mapped, the density figures from the samples were projected to estimate the total amount of aspen available at the colony. Weight of bark available from each diameter class was obtained by referring to measurements made in Minnesota by Aldous (1938). Although growth characteristics of aspen may well be different in the Sierra, the use of Aldous' data was still the most practical method under the circumstances.

Sample plots, 10 by 100 feet in size, were laid out in a direction perpendicular to the shore line and were subdivided into ten, 10 x 10 foot squares. On the yearly runs of these samples, conducted at the end of August or early in September, note was made of the number and diameter of trees standing and felled on each 10 x 10 foot subsection. Placement of these "spoke" samples was not random. Instead, one or more plots were established in each large aspen stand, the number of plots depending upon the size of the stand. A deliberate effort was made to place the plot so that it would be as representative as possible of that stand. Locations of all these samples are shown on the maps of the colonies (Fig. 2).

On each visit to a colony the diameters of all newly-cut aspen trees were measured at stump height. As a stump was tallied it received a mark of red paint so that it would not be mistaken for a fresh cutting on subsequent visits. When cutting was at a maximum during the summer and early fall, visits were frequent, sometimes as often as once a week. In the winter, visits were at intervals of about 6 weeks. Every effort was made to find, mark and measure all trees cut since the previous visit. Because of the ease of finding newly-cut stumps and because re-runs made the same day rarely turned up stumps overlooked on the first run, it is believed that these counts are over 90% accurate and complete.

This method, which is essentially that used in a similar study by Aldous (1938), was used at the Upper and Lower colonies to determine absolute rates and amounts of aspen felled. At the Rockslide colony aspen use was so light that it was computed solely on the basis of the yearly runs of the samples already described.

Supply of aspen in the 3 colonies

The amount of aspen in the immediate environs of the colonies can be judged from a glance at the maps. Aspen cover at the Upper colony was extensive. There was very little of this species at the Rockslide colony and a moderate amount at the Lower colony.

TABLE I. Number of aspen trees within 100 feet of Pond

Year	COLONY		
	Upper	Rockslide	Lower
1953	3180	400	3160
1954	2700	250	2190
1955	2300	200	1635

The question now arises: just how much aspen at a given colony is reasonably accessible to beaver? The tree growing 100 yards from shore can not be considered to be as available as one at the water's edge. Although distance from water certainly must decrease availability, somewhere it is necessary to draw an arbitrary line within which to confine the measurements. Hodgdon and Hunt (1953) state that beavers rarely traveled more than 100 yards from water. Hammond (1943) observed that they traveled 200 yards. Bradt (1938) considered that ordinarily 200 feet was the limit, but mentioned an instance of a beaver cutting aspen as far as 650 feet from shore. Only one of the 5 colonies studied by MacDonald (1956) cut 200 feet from shore, the average maximum distance being a little less than 150 feet. For the purposes of this study, however, I confined my measurements of aspen availability and aspen use to the zone within 100 feet of the stream since at least 90% of the cutting occurred this close to water.

Estimates of the aspen supply within 100 feet of shore in terms of numbers of trees are summarized in Table I.

Although the figures in this table portray the general trend of availability at each colony, a more accurate comparison is obtained by computing the weight of bark and twigs available from these trees. Such a comparison takes into consideration the differences in amount of food in trees of different diameters. Aldous (1938) and Stegeman (1954) determined the weight of bark and twigs available for aspen of various diameters. Figure 4, which compares availability of aspen among the 3 colonies on the basis of this criterion, was computed by applying Aldous' findings to these data.

Figure 4 shows that aspen supplies were shrinking at all colonies. By 1955 when this study terminated aspen was largely gone from the Rockslide and Lower colonies. The good supply at the Upper colony was dwindling.

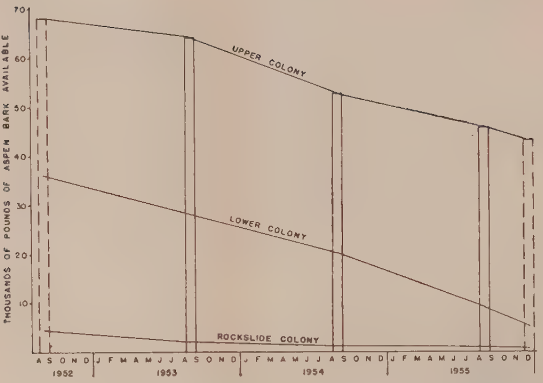

FIG. 4. Aspen availability in terms of green weight of bark and twigs. Dry weight is approximately 60% of green weight.

Distance from shore and relative use of aspen

Subdividing each spoke sample into 10, square sub-samples permitted an analysis of the relation of proximity of water to cutting at the 3 colonies. The results are shown in Figure 5. As would be expected, there is a trend for heaviest cutting to occur close to shore. A similar trend was noted by MacDonald (1956) in Colorado. It is also evident that the beaver will extend their operations farther from shore where the supply is much depleted, as at the Rockslide, than in a situation where aspen is abundant.

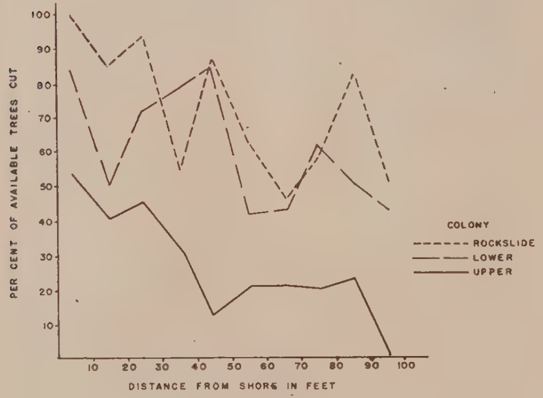

FIG. 5. Relationship between distance from shore and aspen use.

Seasonal cutting of aspen

Figures 6 and 7, based upon total counts, present distribution of aspen use at Upper and Lower colonies by year and by season.

The most striking feature of Fig. 6, in which rate of use is expressed as trees cut per day, is the high rate of cutting at the Lower colony compared to that at the Upper colony. This disparity is explained partly by the larger number of beaver at the Lower colony, but also it reflects the fact that beaver there felled a large number of relatively small trees whereas at the Upper colony fewer trees of larger average diameter were felled.

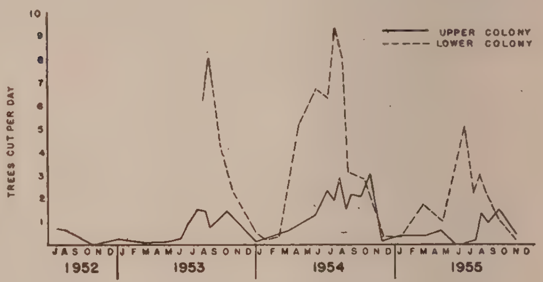

FIG. 6. Aspen use: trees cut per day.

To obtain a truer picture of the amounts of potential food handled at the 2 colonies it was necessary to compensate for the differences in average diameter of aspen felled. The conversion from trees cut per day to weight of bark and twigs cut per day is shown in Fig. 7.

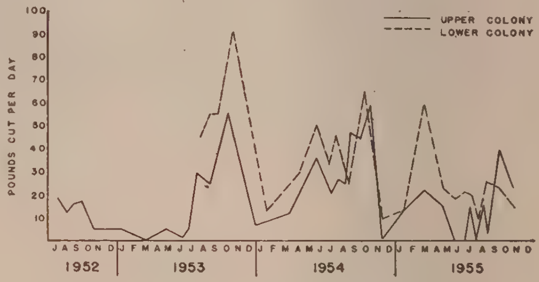

FIG. 7. Aspen use: bark and twig weight cut per day.

From this figure it is evident that the beaver at the Upper and Lower colonies are utilizing the aspen resource in nearly synchronous fashion. The major peak of activity in both areas occurs in late fall, and the time of minimum cutting is in mid-winter. These phenomena are timed by major seasonal changes in the weather. But within the periods of most active cutting the beaver appear to work in minor fits and starts which often are closely synchronized between colonies. I was unable to correlate these minor activity rhythms with changes in temperature or precipitation.

The period of most intensive cutting characteristically occurs in October when the food-pile is being built and dams and lodges are under repair. This trend is reflected in the major peaks referred to above and is in accord with the observations of most naturalists. An exception was found at the Lower colony in 1955 when most aspen was cut in March. There is no obvious explanation for this exception but it is noteworthy that the beaver at the Upper colony also engaged in considerable cutting at this time.

The statement that mid-summer is the period of minimum cutting is frequently encountered. With one exception this situation did not hold true for the Sagehen colonies. Here the beaver usually fell a large portion of the season's quota during the summer. They cut least from December to March. The exception occurred at the Upper colony in the 1955 season when beaver felled no aspen whatsoever during the month of June. The fact that no kits were produced in this colony in 1955, due to the accidental death of the breeding female the previous season, may have been significant. These circumstances suggest that feeding of the kits may have a bearing on the mid-summer cutting of aspen.

Rates of use per beaver-day

As is evident in Fig. 7, the total quantity of bark and twigs from trees felled by beavers of the Lower colony exceeded that of the Upper colony both in 1954 and 1955. The actual ratio for both years was about 1.5 to 1. When account is taken of the number of beaver in each colony, on the other hand, it is apparent that the most aspen use on a beaver-day basis occurred at the Upper colony. A comparison of the three colonies for the years 1954 and 1955 is shown in Table II.

TABLE II. Pounds of aspen bark* cut per beaver day

Colony	1954	1955
Upper	6.2	5.4
Rockslide	0.65	0.03
Lower	3.7	2.1

* Computed by use of Aldous' (1938) conversion factors.

The most important point to be made regarding these figures is the relationship between availability and utilization; the quantity cut per beaver-day was greatest at the Upper colony where availability was greatest and least at the Rockslide colony where availability was least. This is shown graphically in Figure 8.

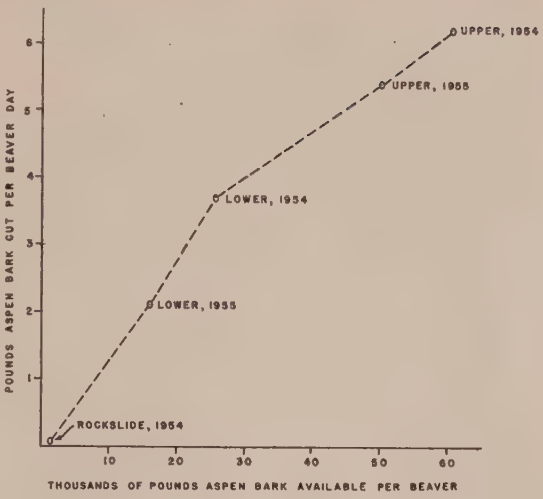

FIG. 8. Relationship between use and supply of aspen.

In using the word "utilization" it should be emphasized that beaver seldom eat all the bark from felled aspen. The unused amount varies with the size of the tree and depends also upon where it falls. Although the exact amount wasted was not determined for the Sagehen colonies, it was noted that beaver usually completely stripped bark only from branches or trunks up to 3 inches in diameter. If a large aspen happened to fall very near the water, however, almost all the bark was removed. Gese and Shadle (1943) stated that the bark of larger limbs is avoided by beaver because it tends to become corky.

MacDonald (1956) found that the average amount of bark used was 87% of that cut. Bailey (1927) estimated use as 50% and Aldous (1938) calculated the average use to be 36%. A figure of approximately 50% might be considered a compromise. Thus of 6.2 pounds of aspen bark cut per beaver-day at the Upper colony in 1954, 3.1 pounds is the estimated consumption. Stegeman (1954) listed 4.5 pounds per day as an average ration, derived from the work of several investigators who kept beaver in captivity. The estimate of about 3 pounds per day, which represents the closest approach to a pure aspen diet attained on this study area, compares favorably with Stegeman's estimate in view of the fact that other foods are always taken to some degree by beavers in the wild.

Size preference

The observation that beaver waste relatively more bark of large trees than small ones leads naturally to the question of preference. Do beaver tend to select aspen of one size class more frequently than others or is the pattern of cutting dictated primarily by relative availability of trees present? An analysis of preference in the field is not simple. Many factors such as local topography, distance from lodge or bank burrow, visibility or natural obstructions in addition to simple numerical abundance undoubtedly interact to influence a beaver's choice of which tree to cut. Since isolation of all the contributing factors is almost imposible in the field, I considered only the most obvious one, numerical availability.

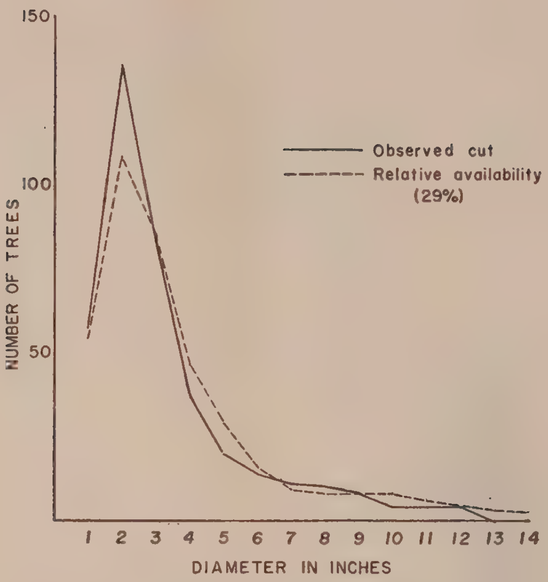

Fig. 9. Relationship of relative abundance of aspen of various diameters to number of trees cut.

Figure 9 summarizes the analysis made at the Upper colony. This graph is drawn from a complete count made in July of 1952. On this count every tree, cut or standing, within the area of use was tabulated. Area of use for this count was arbitrarily defined as the area extending from the water's edge to the most distant trees felled. The relative availability curve on this graph is a reflection of absolute abundance of the various diameter classes before the arrival of beavers.

It will be seen that use of 2-inch trees shows the greatest departure from the availability curve. More than 1300 trees were measured during the count and this departure, though small, proves to be significant at the 0.01 level when subjected to the Chi-Square test for homogeneity. The results of analyses of preference at the Upper and Lower colonies made by means of the spoke samples are similar but, being based on much smaller numbers of trees, are not significant at the 0.01 level.

Preference for trees of this size was indicated by Aldous (1938) and Hodgdon and Hunt (1953), although availability was not specifically documented by them. MacDonald (1956) concluded from his detailed study in Colorado that trees in the 1-3 inch category were preferred.

An attempt to explain this preference poses some interesting problems. The superiority of any size class could either be based primarily on its value as food or as building material. Since this preference for 2 inch trees appears to show a correlation with the amount of building going on at a colony, the latter alternative is favored. It was more marked at the Lower colony which was in a state of rapid expansion during the period of study than it was at the more stable Upper colony. Furthermore, as building declined during the period of study at the Upper colony, the differential preference for small trees also diminished. MacDonald (1956) noticed a similar situation in his most actively expanding colony, where cutting of 1-3 inch trees was very high.

Impact of beaver on aspen

Aspen cannot be regarded as a "renewable resource" within the probable life of any single beaver colony. The aspen steadily declines under pressure of beaver use, even in a situation where the supply is optimum.

The greater the supply of aspen at a colony, the more intense is the effort of the beavers to make use of it. Consequently, the amount of available aspen may be used as an index to the rate of consumption per beaver although it is not necessarily an index to the rate of depletion of the colony's supply.

Furthermore, the size composition of the stand is relatively unimportant since size-preference, though demonstrable, is very slight.

Hence, what might be described as the "aspen-consumption phase" in the life of a beaver colony is a youthful and transitory stage since aspen and beaver, in any combination, inevitably leads to relatively complete loss of aspen. Gradually the colony passes on to one of several more mature phases.

Willow

Willow is the 2nd woody staple of beaver diet, and it can sustain the animals in the absence of aspen. The Rockslide colony, for example, subsisted almost entirely on willow during the study period and a new colony became established early in 1954 near the mouth of Sagehen Creek far from any aspen. Since the Upper, Rockslide and Lower colonies differed so markedly in respect to willow supply, it became clear that a comparison of its use should be made to supplement the study of aspen use started first.

Methods

Sampling of willow was begun in 1954 and continued more intensively in 1955. Transverse plots measuring 100 by 10 feet were marked out across each colony, usually at 125 foot intervals (Fig. 2). The plots were subdivided into 10 sections, each 10 x 10 feet. A willow clump having more than half of its base within the boundary of the plot was considered "in" and its projected area was sketched on a diagram of the plot. These sketches were useful in measuring the proportion of each plot covered by willow. In the Lower colony the plots were in some cases much farther apart than 125 feet. Consequently, the coverage there was estimated to be about 3% in contrast to the 8% coverage at the other 2 colonies.

After fixing the boundaries of a plot, all cut stems ⅛ inch or more in diameter were painted red and on succeeding visits the newly cut stems were tallied and painted. In estimating use from these tallies it was necessary to compensate for variations in the amount of branching. Measurements on a lightly used area showed that, on the average, a vigorous willow stem cut at the usual beaver height of 12 to 18 inches above the ground had 3 branches. Where browsing had been heavy, on the other hand, most of the older, branched stems had already been cut and the beaver were relying on the unbranched shoots which appear annually after browsing.

Consequently a "branching factor" of 3 was applied to the tabulation of use at the Upper and Lower colonies as well as to the stands of vigorous willow on the lower end of the Rockslide colony. On the heavily-used sections of the Rockslide colony no corrective factor was necessary since the willow shoots were largely unbranched.

Availability and use of willow

Table III presents comparative measures of availability and use of willow in the 3 colonies for the period July-October, 1955. According to these figures the Upper colony had the least willow, the Rockslide colony an intermediate amount and the Lower colony the most. Percentage use was high at the Upper and Rockslide colonies and low at the Lower colony. If use is computed on a per beaver-day basis to compensate for the effects of different population size, the rate of consumption at the Rockslide colony is high, that at the Upper and Lower colony is low. There certainly is no obvious relationship between supply of willow and rate of use. Both the crude and more precise measures of use demonstrate that consumption was highest at the Rockslide colony where the supply was intermediate.

It should be pointed out that the high figure for the Rockslide colony is partly explained by extraordinary dam-building activity there. During the 1955 season these beaver were attempting to maintain a dam across the Hobart Mills water intake. Each time the dam was removed it was rebuilt by the beaver. However, when a reasonable allowance is made for the extra willow cut exclusively for construction, the trend for heaviest consumption per beaver-day at this colony is unchanged.

Table III. Supply and use of willow, by colony

	Colony		
	Upper	Rockslide	Lower
pounds bark available in July	570	2,040	11,580
pounds bark cut July-October	229	906	992
% cut	40	44	9
pounds bark cut per beaver-day	0.67	1.54	0.76

Role of aspen supply

Since Table III indicates that willow use is not obviously dependent upon the supply, there must be other controlling factors. One good possibility would be the amount of aspen cut in the various colonies. The amount of aspen cut per beaver-day during this same period was 6.7 pounds at the Upper colony, 0.1 pound at the Rockslide colony and 1.9 pounds at the Lower colony. A comparison of these figures with those for willow use is shown in Figure 10 and suggests an inverse relationship between consumption of aspen and willow. The data indicate that where most aspen is cut, as at the Upper colony, least willow is cut and where aspen consumption is least, as at the Rockslide colony, willow is most heavily used. Since the amount of aspen cut in turn depends upon the aspen supply (Fig. 8), we may go one step farther and say that use of willow is also inversely related to the supply of aspen. This is equivalent to saying that the supply of aspen controls in some measure the consumption of both aspen and willow.

The easiest way to interpret this relationship in terms of the beaver is to assume that they concentrate on the aspen, relying increasingly on willow as the supply of aspen diminishes.

Facets of the availability concept

The fact that aspen is the preferred food raises another question. If, as has been shown by Aldous (1938) and Bradt (1938), beaver may be kept for months on an exclusive diet of aspen, why do the beaver at the Upper colony where the aspen is very abundant bother to consume any willow? The explanation may lie in the intricate interac-

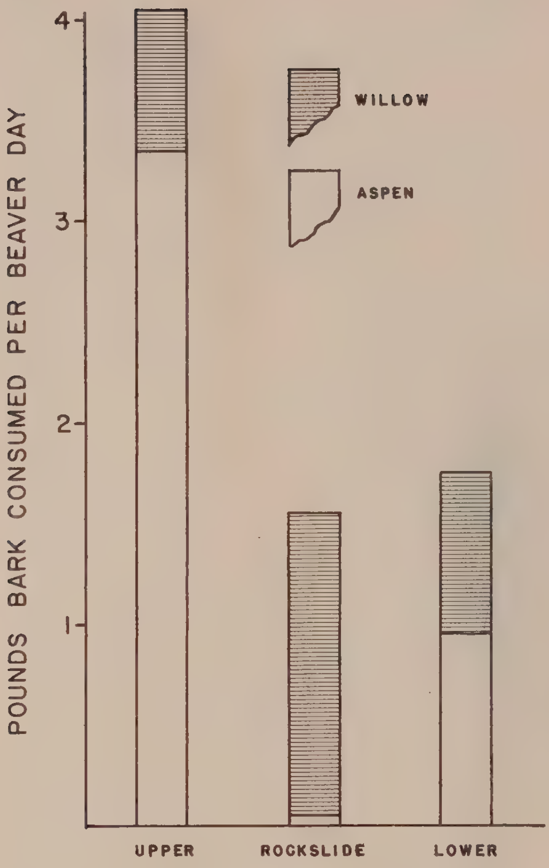

FIG. 10. Use of willow and aspen on the 3 colonies studied, July-October, 1955. Use of aspen estimated to be 50% of the cut.

tion of factors which, together, add up to availability. Factors such as absolute numbers of trees, distance from shore, topography, type of soil and presence and distribution of alternate forage have already been mentioned. Others probably contribute. The one which may explain the consumption of a substantial amount of willow even where aspen is abundant is a temporal factor. Not once during the 4 summers of observation was a beaver actually seen to fell an aspen. This activity was restricted to some time well after dark, when observation was not possible.

It was noted that the usual routine of a beaver upon emerging from the lodge in the early evening was to take a few turns around the pond in a tour of inspection and then to start feeding on willow. The beaver are undoubtedly hungry after a long day of confinement, but do not feel at ease about going ashore to fell or trim aspen until it is completely dark. During this period, therefore, aspen appears to be relatively much less available than willow. The latter may almost always be cut by an animal in the water or a foot or two from shore. That twilight behavior was the same in all colonies, regardless of aspen supply, probably is an important factor in explaining why a certain amount of willow is cut even where it might not appear to be necessary.

Year-to-year effects of beaver activity

It is evident from Table III that there is a downward trend in willow availability at all 3 colonies during the July-October period. But to evaluate the total effect of beaver one should consider a year-long record in which such factors as sprouting and die-back are also taken into account.

Die-back of willow occurred in all colonies observed and was also seen in willow untouched by beaver. Most of the die-back is thought to take place during the winter and it is encouraged by over-browsing. Actual removal of sprouts by the beaver and the additional loss by die-back constitute the "loss factors" affecting availability. Sprouting during late May and early June is the major "gain factor."

The amount of willow available fluctuates from year to year and within the seasons of every year, increasing when the gain factors outweigh the loss factors and decreasing when the loss factors predominate.

Figure 11 shows details of availability trends in willow on one of the intensive samples at the Rockslide and one at the Upper colony during a single year. Both graphs in this figure are similar in indicating that the willow supply in October, 1955, was below the October, 1954, level. Beaver use had been too heavy for a sustained yield on either area.

In other respects the 2 sample areas represent opposite situations and deserve some comment. The graph for the Upper colony sample indicates that the sprouting was almost sufficient to compensate for the extensive losses due to beaver work and die-back combined. Thus, only a small net loss resulted for the year. This situation is summarized by the columns on the right side of the graph.

At the Rockslide colony, however, it is clear that a heavy net loss occurred although beaver work was rather light. Die-back alone exceeded sprouting and this loss added to the loss due to beaver cutting produced the marked drop seen in the figure.

A vigorous stand can tolerate a rather large harvest by beaver, at least for one or 2 seasons, but willow which has been consistently over-

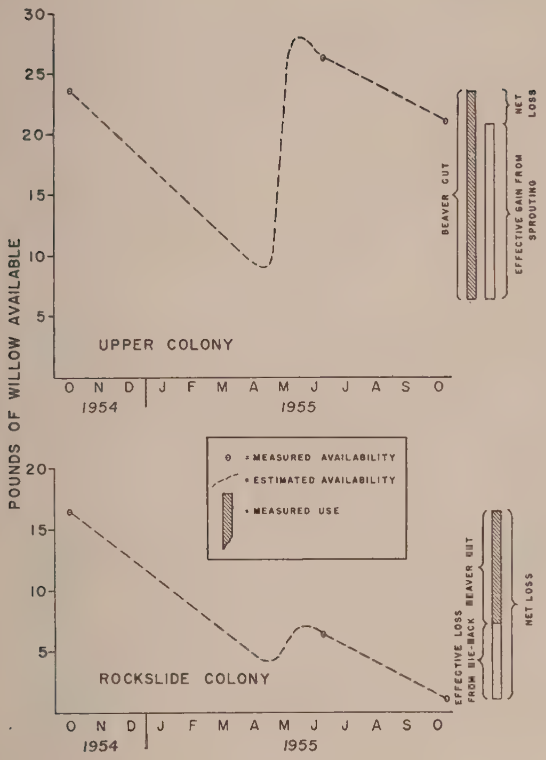

FIG. 11. Trends in willow supply and use on 2 intensive samples.

browsed, as at the Rockslide colony, will decline under a much smaller harvest. The decline in sprouting vigor following overbrowsing is the most significant relationship reflected in Fig. 11.

Although no intensive samples were run on the Lower colony, it seems almost certain that, in contrast to the other 2 colonies, willow was being cut on a sustained yield basis. One index of the condition of a willow stand is the average stem length. Not only was the average stem length greater than at either of the other colonies but, equally important, the July-October harvest, shown in Table III, was much lighter.

In attempting to estimate how much willow can be safely harvested by beaver, it seems clear that vigor of the stand is more important than total supply. MacDonald (1956) recognized this in estimating a safe harvest in terms of the current year's growth, another index of vigor. His suggestion of 20% of the current year's growth as a safe margin seems conservative to me but our data are not directly comparable.

Any estimate of a safe harvest of willow for a particular colony tends to imply that beaver colonies are fixed in location and that they are dependent upon a specific block of willow plants for their sustenance. On Sagehen Creek, where the distribution of willow extends for most of the length of the stream, this certainly is not true. In this type of habitat the beaver will gradually shift the site of their operations up or down stream as willow in the original colony area is overbrowsed. This was seen in a downstream shift of the Rockslide colony in 1954 and 1955. Overbrowsed sites, subsequently abandoned, will soon reproduce a healthy regrowth of willow, as Adams (1954) has noted. Of 29 deserted colonies examined by Haas (1943), only 4 were abandoned because of overuse of willow. The sprouting capacity of this durable plant makes it a mainstay of beaver economy, and even severe abuse will discourage it only temporarily. Seemingly, beaver can thrive indefinitely on willow by a form of "block cutting," or shifting their foraging periodically up and down the stream allowing overbrowsed sections time to recover.

Summary

Two pairs of beaver were introduced on Sagehen Creek in 1945. Ten years later the number had increased to about 30 animals distributed in 5 colonies along the stream. Three of the colonies were studied for several seasons in order to explore the interaction between beaver and their 2 chief food-and-building resources, willow and aspen.

The rate at which beaver cut aspen was found to be correlated directly with the supply. On the other hand, rate of willow use showed no correlation with willow supply but was related inversely to aspen supply. These relationships are interpreted to mean that aspen is the first choice item; as it is used up the beaver take more and more willow.

According to an analysis at the colony where aspen was most abundant, the principal factor influencing a beaver's choice of size of tree to cut is the relative numerical availability of the sizes in the stand. A slight but significant preference for trees of the 2-inch diameter class was demonstrated. This preference is thought to be due primarily to superiority of 2-inch trees as a building material rather than as a food source.

The exceptional sprouting vigor of willow makes it much more tolerant of the inroads of beaver activities than is aspen. Even so, beaver have a tendency to overbrowse within the immediate colony area. The result is that sprouting vigor gradually declines and rate of growth falls behind rate of harvest.

Use of aspen never is on a sustained yield basis.

When beaver have consumed the aspen in one locality it is gone. Willow resprouts much more successfully than aspen, but the beaver still tend to eat it more rapidly than it grows. However, as one site becomes exhausted of willow, the beavers shift gradually up or downstream to better stands, thus permitting the original area to recuperate. Consequently, in terms of the entire stream, the willow is on a sustained use basis in a manner analogous to block-cutting as practiced by foresters. Whether it will remain so as the population continues to increase and expand into all habitable areas of Sagehen Creek cannot be foreseen.

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A MECHANICAL MODEL FOR THE STUDY OF POPULATION DYNAMICS

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INTRODUCTION

The machine described in this report was constructed at a time when analog computers were becoming fashionable. I had hoped to use it in a study of the complex changes in population structure that accompany changes in the reproductive rates and mortality rates of different age classes of populations of small mammals. It soon became apparent that the machine was capable of "solving" various kinds of problems put to it, but that preparation and calibration of the machine for each problem was too time-consuming to make

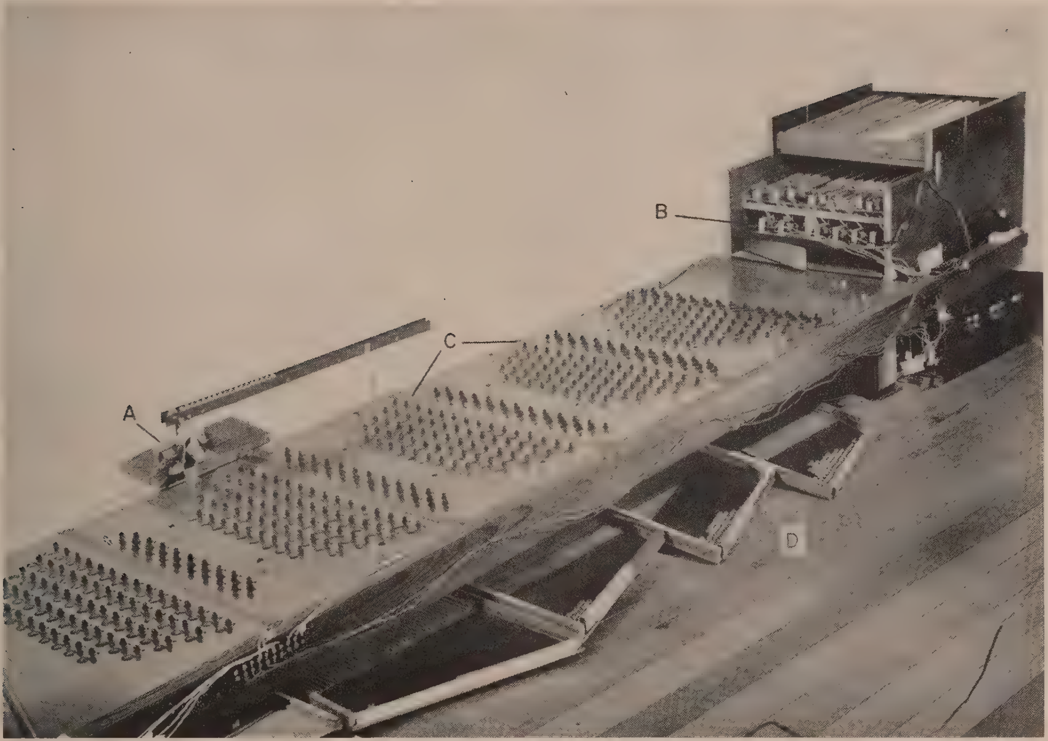

FIG. 1. The machine, showing the 5 fields of pegs and holes. A. Solenoid and supply of balls for automatically replacing balls that survive through all 5 fields. B. Solenoids and supply channels for automatic release of litters when balls cross the breeding strips. C. Two of the 4 breeding strips. D. Trays for catching and displaying balls that have fallen through holes.

it useful for solving with dispatch a series of problems. More important, it soon became apparent that for not a single species of wild mammal were there adequate field data to feed into the machine to enable it to analyze to the full limit of its ability the population problems for which it was designed. In the process of putting questions to the machine, however, the operator frequently became aware of various aspects of the problem that might otherwise have been overlooked. To be sure, an astute mathematician could have foreseen all of these possibilities and made room for them in appropriate equations, but for the ordinary mathematically impoverished field biologist the machine proved to be a valuable intellectual crutch. It is also a stimulating teaching device that gives one the intellectual and esthetic satisfaction (and excitement) of being able to watch a population responding to the various aspects of reproduction and mortality that tend to keep its numbers in equilibrium.

It should be pointed out that I have designed the machine to function in the manner that I believe populations function in the wild. Consequently, it is nothing more than a mechanical expression of my own notions about populations and as such is perfectly capable of reproducing over and over all of the misconceptions of its designer.

THE MODEL

Essentially the model consists of a long inclined plane into which a large number of holes has been drilled and down which balls are permitted to roll. It resembles a metamerically elongated pinball machine (Figure 1). As long as it remains on the surface, the ball represents a living animal; when it falls through a hole it represents a dead animal. Balls that "survive" long enough are permitted to "reproduce," thereby contributing to the maintenance of the population. Numerous embellishments, however, are necessary before the model becomes rewardingly analogous to a wild population, and these will be described below.

Mortality

The inclined plane or "board" is a 2 x 8 foot smooth piece of formica mounted on ¾-inch plywood. The holes, which provide mortality because through them animals are removed from the population, are ¾ inch in diameter and carefully

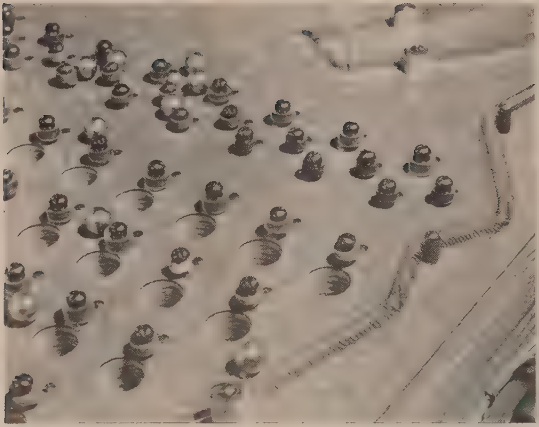

FIG. 2. Close-up view of part of one of the fields showing pegs, holes, and ½-inch steel balls.

drilled and reamed so that they have no raised lip and no saucered rim. On the up-hill side of each hole is a carefully placed peg (Figure 2). The pattern and spacing of the holes and pegs were arranged, after preliminary tests, to make it unlikely that a ½-inch steel ball rolling down the board by itself would enter a hole. To make this low mortality possible, a ring of tygon plastic tubing was placed around each peg. This plastic imparts almost no bounce to the balls and allows them to follow a course like that of ball A in Figure 3. If it is desired to increase mortality, some or all of the tygon bumpers can be replaced with rubber bumpers (Xs in Fig. 3), which will bounce many of the balls off of the safer path, or some of the pegs can be removed completely permitting the balls to drop directly into the holes (large black discs in Fig. 3).

Three categories of mortality are involved in the operation of the model: proportional, compensatory, and density independent. Note that the manner in which I use these terms below differs from the confusing usage of some authors today. The model inflicts a fixed, proportional mortality on the population of balls simply by "swallowing" more balls when the population increases. No course down the board is completely safe, so the more balls that attempt the course the more will fall through the holes. Proportional mortality can be increased by removing some of the pegs that protect the holes or by substituting rubber for plastic bumpers on the pegs.

When a single ball rolls down the board it has, because of the arrangement of pegs shown in Fig. 3, the greatest probability of survival if it is undisturbed during its passage. When the population of balls is high, however, the probability is increased that some other ball will bump it off of the safest route and into one of the holes (ball B in Fig. 3). This provides compensatory mortality: the more balls present at one time the more they will bump each other, and the more they bump the higher will be the mortality.

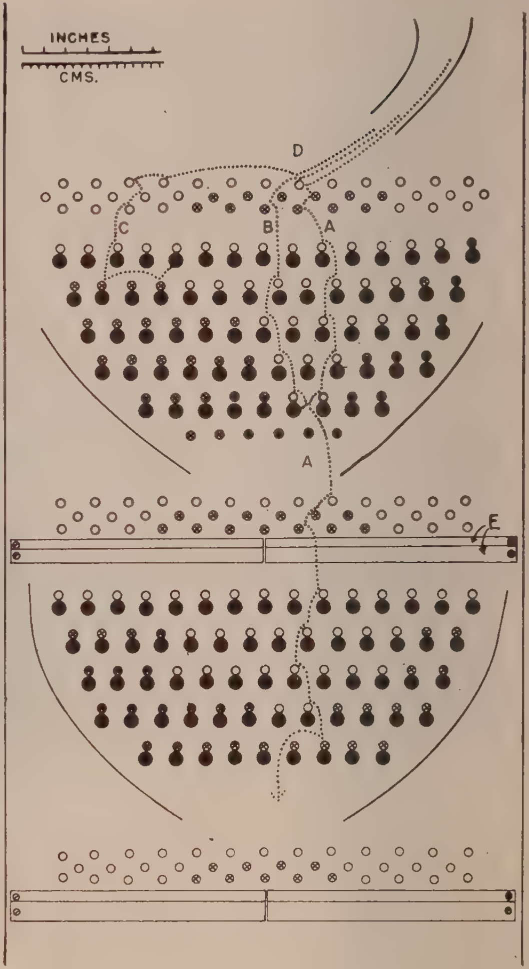

FIG. 3. Diagram of the pattern of the first 2 fields. Dotted lines show the course taken by balls under different circumstances explained in the text.

A 2nd method of carrying out compensatory mortality has also been provided. When balls are released onto the board (= birth or weaning), they sweep in from one side toward a triple row of pegs (Fig. 3). These pegs are spaced far enough apart so that balls can easily fit between them but closely enough so that the balls take considerable time threading their way through the maze of pegs. Consequently, when populations are high and a great number of balls are being born a traffic jam develops at D in Fig. 3. As long as congestion persists at D, many of the new arrivals bounce off of their predecessors toward the farther side of the board (ball C in Fig. 3), but many of the pegs on the farther side of the board are provided with rubber rings, which makes passage down that side of the board much more dangerous. Consequently, when populations are high many balls are rerouted to a more dangerous path, thus providing additional compensatory mortality. This corresponds in nature to young animals, when populations are high, being forced to establish themselves in submarginal habitats where the probability of death is much higher than in the more suitable habitat already filled to carrying capacity by their predecessors.

Density independent mortality consists of the death of a fixed number of individuals per unit of time irrespective of the number of individuals existing in the population. No automatic mechanism for carrying out density independent mortality was incorporated in the mechanical model because most zoologists believe that little of the total mortality is truly independent of density. One can, however, introduce this kind of mortality while the machine is operating simply by removing by hand the desired number of balls per unit of time.

I have used the machine only for problems in which males were assumed to have the same mortality as females. It would be possible, however, to represent males by balls that were heavier, lighter, larger, smaller, more or less lopsided than those representing females, and this would provide different mortalities for the two sexes.

Reproduction

If one of the steel balls eludes all of the holes in one "field," it comes, after being slowed and its path straightened by a filter of pegs, to two strips of bronze (E in Fig. 3). It rolls smoothly onto one of the strips, then must mount about 1/32nd of an inch onto another bronze strip. During the instant that the ball touches both strips an electric circuit is completed that sends an impulse to a multivibrator circuit through which the impulse is lengthened, amplified, and fed to one or more electro-mechanical solenoids. Each time one of these solenoids is activated it pokes a waiting steel ball out of a tube. The ball then rolls out onto the board, completing the "birth" process.

The model was constructed to accommodate 6 solenoids each of which could expel balls from 2 storage tubes. Accordingly, each ball crossing the bronze "breeding strips" is capable of producing 1 to 12 offspring depending upon the wishes of the operator. Since, in nature, males do not bear offspring, a certain percentage of the steel balls can be lacquered so that they will not carry the electric current that activates the reproductive machinery. The percentage lacquered would depend upon what sex ratio one wished to have in the breeding population. For many problems in which a 50:50 sex ratio is acceptable, one can permit males as well as females to reproduce, in which case the number of balls born must be cut in half to compensate for the doubled number of breeding individuals. Under these conditions the release of 12 balls at each crossing of the breeding strip is the reproductive equivalent of the production of litters of 24 by females only.

It may be seen in Fig. 1 that the board consists of a series of 5 fields with a breeding strip at the bottom of each field. The balls on each field represent one age group of a population. Those balls that survive the mortality prepared for them in one field then automatically cause litters of a predetermined size to be released onto the first (juvenile) field while the parent balls face the mortality that has been prepared for them before their next period of reproduction. Note that different mortalities can be provided for each field (= each age class) and different litter sizes for different age classes as well. Any ball that survives all 5 fields to reach the bottom of the board activates a separate solenoid that feeds a similar ball across the last breeding strip onto the last field. Long-lived individuals, therefore, are recirculated through the last field and are subjected to the rate of mortality appropriate for old animals until they finally drop into one of the holes.

It should be pointed out that if 2 balls cross a breeding strip at the same instant, only one litter will be produced. Because of inertia in the reproduction mechanism, the refractory period after the passage of one ball amounts to a small fraction of a second during which further reproduction by balls crossing that strip is not possible. This results in a compensatory reduction in reproduction similar to that found in populations of certain species when numbers are excessive. On the model this effect can be altered in 2 ways. The breeding strip at the bottom of the first field, which always carries the densest population, can be divided into 2 or more separate sections, each section connected with a separate reproducing solenoid, or solenoids. This results in each circuit serving only half, or less, of the traffic, thereby raising the population level at which appreciable amounts of reproductive failure occur.

If it is desired, one can alter resistances in the multivibrator circuits and thereby change the refractory period that follows the passage of each ball across the breeding strips.

Census

While the model is in operation balls are rolling down the board, dropping through the holes, and being replaced with such rapidity that it is not possible to count the population. Accordingly, if a census is desired it is necessary to mount a 35-mm camera or a single-framing motion picture camera above the board and to photograph it at appropriate intervals. Then the films can be projected and the population existing in each of the 5 age classes can be counted. Balls falling through the holes in each field are directed into separate trays where they too are visible in the photographs and can be counted in order to arrive at a figure for the total amount of mortality that has occurred in each of the age classes. A clock readable to seconds should be visible in each photograph.

AN EXAMPLE

Suppose one desires to investigate the effect of various changes of litter size on the size and age composition of a population of some species of animal living under a fixed program of mortality. We decide to subject the young animals between birth and the production of their first litter to a 72% proportional mortality, a low compensatory mortality, and no density independent mortality. The older animals, we decide, will also be subjected, in the period between the production of successive litters, to a 63% proportional mortality, a low compensatory mortality, and no density independent mortality. Notice that mortality is expressed not in periods of time but in breeding periods, or generation periods, and that the periods may be different in different age groups. For the sake of simplicity we might assume that the species under consideration produces one litter per year and that the young reproduce when they are one year old; under these assumptions each field along the board would represent one year.

Before setting the machine into operation, it is necessary by the proper positioning of tygon and rubber bumpers, to arrange for the 72% and 63% proportional mortalities. When the proper arrangement has been achieved, a great number of balls can be rolled down the board one by one and 72% of them will fall through holes in the first field and 63% of those entering each of the succeeding fields will fall through holes. Provision for the desired degree of compensatory mortality is made on the basis of previous experience, but the exact amount of compensatory mortality actually achieved will not be known until after the run because one does not know beforehand what the population density will be—and this affects the compensatory mortality. After the mortalities are arranged for, the reproduction strips can be connected to the appropriate number of solenoids to give the desired litter size. The model is then set in operation by "seeding" the board with a number of balls. If the litter size is large enough the population will increase and then fluctuate around an equilibrium; if the litter size is too small to overcome the total mortality, the population will die out. Compensatory mortality and compensatory reduction of reproduction are the features that enable the model to attain equilibrium. Either one alone is capable of imposing equilibrium. For simplicity, we shall ignore compensatory reduction of reproduction in this example.

Figure 4 summarizes the results of a series of runs with different reproductive rates but with the fixed mortality program assumed in the preceding paragraph. It may be seen that the population could not maintain itself when the reproductive rate was 8 per adult ball but with the young in the first field not breeding at all (abbreviated 0/Y + 8/A). Several trials were made at this reproductive rate but in each trial the population died out (line B in Fig. 4). However, when the reproductive rate of the adults was raised to 10 (0/Y + 10/A), the population survived, although barely, for at one point mortality had reduced it to a single individual (line A in Fig. 4). When the young were permitted litters of 1, a litter size of 6 for adults (1/Y + 6/A) was adequate to maintain the population. On the other hand a litter size of 5 for young individuals was adequate to maintain a population without any breeding by adults (5/Y + 0/A). Four per young would not maintain a population, but 4/Y + 1/A maintained a fairly stable population (lines E and D in figure 4). Increasing the litter size of adults by steps of 1 then increased the equilibrium population accordingly by small amounts (line C in figure 4). When the litter size of young was increased from 5 to 6 (6/Y + 0/A) the level of equilibrium increased, even without any offspring from adults, to more than 140.

Analysis of the records of the populations at equilibrium under the above program of mortality shows that approximately one to 5% of the total

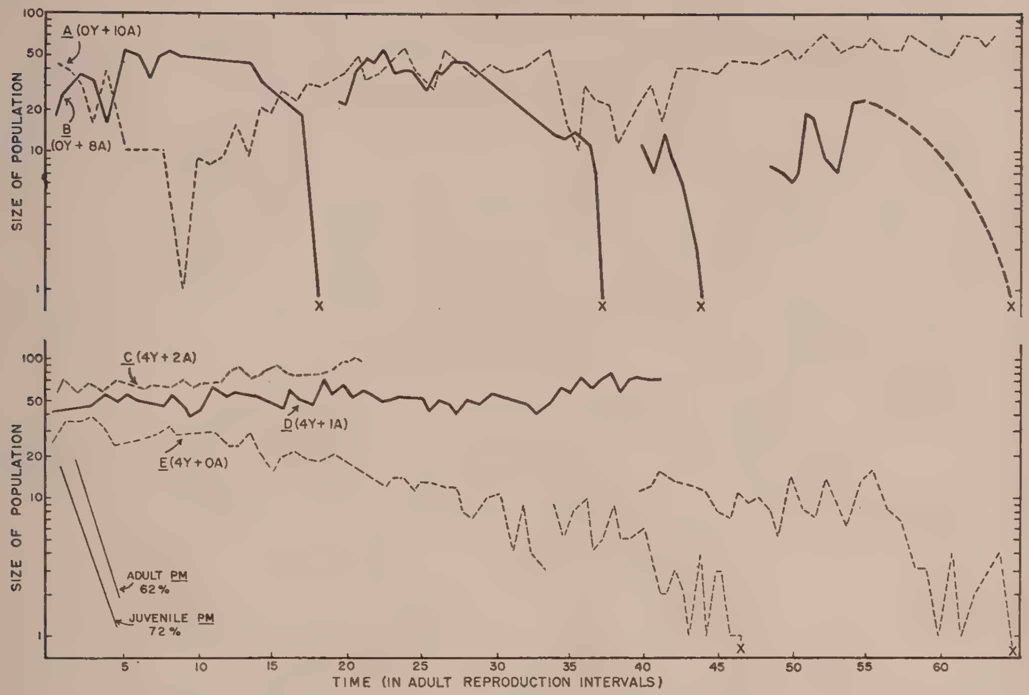

FIG. 4. Size and fluctuation of the population of balls under a fixed program of mortality but under 5 different programs of reproduction.

mortality resulted from compensatory mortality. In the terminology of a later section of this paper, the compensatory mortality exponent for juveniles was very roughly 0.91 and for adults approximately 0.93. It is interesting that no matter what the program of reproduction, the percentage of juveniles in the equilibrium populations remained about the same, 82%. Juveniles are considered to be those between birth and the age of potential production of the first litter (*i.e.* those in the first field).

The lines in Fig. 4 illustrate the fluctuations in the total number of balls on the board for periods of a few minutes. However, since the average time required for a ball to roll from "birth" to the first breeding strip was 7.20 seconds and from one breeding strip to the next was 5.36 seconds, a run lasting 2 minutes is analogous to a span of more than 20 adult breeding periods, or reproduction intervals. For a species that breeds once each year, line A in Fig. 4 would represent the size of the population and the amount of fluctuation that would be expected under the specified program of reproduction and mortality over a span of more than 60 years. Similarly, line D would represent the population level and fluctuation of the same species over a span of 35 breeding periods under a different program of reproduction but the same program of mortality. It will be recalled that the mortality consisted of no density independent mortality, a proportional mortality of 72% between birth and the first breeding period and 62% between each of the succeeding breeding periods, and a low compensatory mortality. The slope of the 2 straight lines to the left of the lower series of graphs shows the rate at which the juvenile and the adult populations would be extinguished by proportional mortality alone if there were no reproduction.

Stability of populations

Figure 4 shows that under some circumstances the size of the population fluctuates rather violently and under other conditions is rather stable. Line D, for example, represents a rather stable population throughout a span of about 40 breeding periods, during which 55 censuses were made. Line A represents extreme variability in population numbers. It is enlightening to examine some of the factors influencing the stability and the instability of such populations.

One factor contributing to the variation in numbers is population size itself. The machine is most useful for dealing with populations smaller than 100, and with populations of this size random fluctuations can be appreciable. Under the arranged program of mortality, a streak of bad luck could easily eliminate a population of 20 balls (see how rapidly the population drops when reproduction ceases). Fig. 4 shows that although many of the populations seem to be well established, fluctuations are great enough in most examples so that in a few thousand more breeding periods an unusually large break in the curve might reach bottom. This would represent extinction of the population through pure statistical probability without any change in the rate of mortality or the rate of reproduction. At first thought it might seem that the machine is of little use because it cannot handle much larger populations than this, but it can be argued that the "world" of most small mammals (and of many other vertebrates) consists of fewer than 100 individuals of their species. Not only do they rarely encounter 100 other individuals, but frequently they live in isolated patches of suitable habitat in which the total population consists of fewer than 100 individuals of their species. It is clear, therefore, that extinction through chance fluctuation is not only a possibility for small populations but, under conditions of mortality and reproduction such as those illustrated in Fig. 4, it is probable over a long term.

Population fluctuations on the board of the mechanical model can be reduced in several ways, both through alterations of reproduction and through alterations of mortality. For example, the coefficient of variation can be calculated for populations such as those graphed in Fig. 4, and it is found to be high in populations that depend heavily on adults for reproduction (such as 0/Y + 10/A; 1/Y + 6/A) and low in populations where young do most of the reproducing. Upon watching the model while it is carrying on the 0/Y + 10/A operation, it becomes obvious why the variation is so high with this breeding program. Mortality is so high among both the young and the adult age classes that few individuals survive long enough to reach the breeding strips. During the 0/Y + 10/A operation there were, on the average, only 6 adults on the board at any one time, and many of these would have perished before they had reached the next breeding strip. Consequently, survival of the population sometimes depended upon the reproductive efforts of only one or 2 individuals—a precarious survival. The situation reminds one of a Lost Battalion staking its survival on 10 rescue messages tied to one homing pigeon rather than on one message tied to each of 10 pigeons. Other things being equal, the population is more stable when a large proportion of the reproduction is carried out by the young, more numerous age class.

Were it not for compensatory mortality (or compensatory reduction of reproduction) the model would not succeed at all; that is to say, it could not keep a population near some equilibrium point. With proportional mortality alone, density independent mortality alone, or any fixed combination of the two, populations would either "run wild" or die out, and one of these 2 events would occur no matter what fixed breeding program was arranged. It follows that the greater the compensatory mortality imposed on the population, the greater will be the stability. Unfortunately it is not possible to prepare the model directly for close imitation of some situation in the wild because for wild populations we do not know how much of the total mortality (even if that is known) is compensatory, how much proportional, and how much density independent.

In the situation illustrated in Fig. 4 with a 72-63% proportional mortality, the compensatory mortality among these populations at average population levels between 15 and 140 individuals varied between one and 5% of the total mortality. The compensatory mortality was higher when populations were high (as it should have been) than when they were low. Judging by the amount of variation in population levels that occurred even in populations that persisted for hundreds of generations, this amount of compensatory mortality is relatively low and under the best of circumstances could not be expected to keep a small population from making wide departures from the equilibrium level. To estimate the amount of compensatory mortality in a wild population, it might be possible to set up the mechanical model in as close imitation of the reproduction and mortality of the wild population as possible and then vary the amount of compensatory mortality until an amount was reached at which the fluctuations of population size on the board, the rate of growth of the population, and the ratio of juveniles to adults were comparable to those of populations in the wild. In this manner the model could be used to estimate for a wild population an important population parameter that would be unobtainable by ordinary field techniques.

Some breeding effects

Certain aspects of the reproductive process have interesting effects on the populations. When the population was being maintained by large litters produced by a few individuals (as in the 0/Y

GENERAL PLAN:	POPULATION AT TIME t_2 = NUMBER OF JUVENILES AT TIME t_2 + NUMBER OF ADULTS AT TIME t_2 $P_{t2} = n_{t2} + N_{t2}$		
NUMBER OF JUVENILES AT TIME t_2 n_{t2}	NUMBER OF THE ORIGINAL JUVENILES SURVIVING PROPORTIONAL MORTALITY ON JUVS. DURING ONE R ① NUMBER OF ORIGINAL JUVENILES CROSSING FIRST BREEDING STRIP DURING ONE R $n_{t1}\left(1-\frac{1}{2}\frac{R}{r}\underline{pm}\right) - \frac{R}{r}\left[n_{t1}\left(1-\frac{1}{2}\underline{pm}\right)+\frac{1}{2}\underline{dim}+\frac{1}{2}\left(n_{t1}-n_{t1}^{\underline{cme}}\right)\right]$	NUMBER OF ORIGINAL JUVENILES SURVIVING $\underline{pm}$ AND NOT YET HAVING REACHED BREEDING STRIP AT TIME t_2 ⑥	1
	NUMBER OF ORIGINAL JUVENILES CROSSING FIRST BREEDING STRIP DURING ONE R $+\left\{\frac{R}{r}\left[n_{t1}\left(1-\frac{1}{2}\underline{pm}\right)-\frac{1}{2}\underline{dim}-\frac{1}{2}\left(n_{t1}-n_{t1}^{\underline{cme}}\right)\right]\ell\cdot♀\cdot\underline{bc}\right.$	NUMBER OF OFFSPRING PRODUCED BY JUVENILES DURING ONE R	2
	NUMBER OF ADULTS CROSSING A BREEDING STRIP DURING ONE R $\left.+\left[N_{t1}\left(1-\frac{1}{2}\underline{PM}\right)-\frac{1}{2}\underline{DIM}-\frac{1}{2}\left(N_{t1}-N_{t1}^{\underline{CME}}\right)\right]L\cdot♀\cdot\underline{BC}\right\}$	NUMBER OF OFFSPRING PRODUCED BY ADULTS DURING ONE R	3
	PROPORTIONAL MORTALITY ON OFFSPRING DURING R ② — $\underline{dim}$ ON ALL JUVENILES DURING ONE R — COMPENSATORY MORTALITY ON ALL JUVENILES DURING ONE R ③ $\left\{1-\frac{1}{2}\frac{R}{r}\underline{pm}\right\} - \frac{R}{r}\underline{dim} - \frac{R}{r}\left(n_{t1.5}-n_{t1.5}^{\underline{cme}}\right)$	SURVIVORS OF OFFSPRING MINUS ALSO THE $\underline{cm}$ ON PERSISTING JUVENILES, WHICH WAS NOT DEDUCTED IN LINE 1. TOTAL TO HERE (LINES 1 + 4) IS NUMBER OF JUVENILES AT TIME t_2	4
NUMBER OF ADULTS AT TIME t_2 N_{t2}	NUMBER OF ORIGINAL JUVENILES CROSSING FIRST BREEDING STRIP DURING ONE R ④ — $\underline{PM}$ ON ORIGINAL JUVENILES AFTER THEY BREED $+\frac{R}{r}\left[n_{t1}\left(1-\frac{1}{2}\underline{pm}\right)-\frac{1}{2}\underline{dim}-\frac{1}{2}\left(n_{t1}-n_{t1}^{\underline{cme}}\right)\right]\left[1-\frac{1}{2}\underline{PM}\right]$	JUVENILES SURVIVING $\underline{PM}$ AS ADULTS AT TIME t_2	5
	ORIGINAL ADULTS SURVIVING $\underline{PM}$ — $\underline{DIM}$ ON ALL ADULTS — $\underline{CM}$ ON ALL ADULTS DURING ONE R ⑤ $+N_{t1}\left(1-\underline{PM}\right) - \underline{DIM} - \left(N_{t1.5}-N_{t1.5}^{\underline{CME}}\right)$	SURVIVING OLD ADULTS MINUS ALSO THE $\underline{CM}$ ON JUVENILES THAT BECAME ADULTS DURING ONE R. NUMBER OF ADULTS AT TIME t_2 EQUALS LINES 5 + 6. TOTAL TO HERE (LINES 1 + 4 + 5 + 6) IS TOTAL POPULATION AT TIME t_2	6

TABLE I. Formula for calculating the number of animals in a population after a time span of one adult reproduction interval

+ 10/A example mentioned above), it could be seen clearly that the 10 young born at the same moment were subjecting themselves to higher compensatory mortality than would have happened to an equal number of young born in several litters spread over a longer period of time. Production of large litters therefore is inefficient (other factors being equal) in species in which the young are subjected to relatively high compensatory mortality. Lack (1954) has called attention to the low survival of individuals in large litters. Furthermore, it would seem grossly inefficient for all the females of a species to bear young at the same season. Since nature does not make mistakes in such matters and since in many species the females *do* all bear at the same season, it would seem reasonable to assume that in the species in which this occurs, either compensatory mortality is not great at the season of reproduction or that other advantages outweigh increased compensatory mortality. Darling (1938) describes a situation among synchronously breeding birds

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[1] The full proportional mortality does not apply because many balls have already passed many of the holes when the measuring period begins (hence the ½), and because the proportional mortality is active for only R time units instead of r (hence the $\frac{r}{R}$ in this and in the subsequent expressions).

[2] The full proportional mortality does not apply because many balls are not born until late in the measuring period.

[3] It would be desirable to apply the compensatory mortality to the average number of juveniles existing on the board at one time between t_1 and t_2, but this number cannot be known without knowing the answer we seek. A useful estimate, however, is the sum of the calculations up to this term; in other words, the number of offspring produced during R, minus the proportional mortality on them, minus the density independent mortality on them, plus line 1. Use of this estimate does not affect the accuracy with which the population level at equilibrium can be predicted, but it does alter slightly the speed with which equilibrium is reached.

[4] The value of this expression will have been calculated already in both line 1 and line 2.

[5] As in footnote 3, an estimate must be made of the population to be subjected to compensatory mortality. A useful estimate is line 5 plus line 6 up to the final pair of parentheses.

[6] Some of the expressions can be simplified considerably, thereby making the calculations less tedious. The entire formula also can be programmed for rapid iterative solution with a digital computer.

in which compensatory mortality (at least as far as predation is concerned) is minimized by "saturating" the predators.

Colonization

Conservationists and evolutionists sometimes wish to calculate the probability that a single or a few individuals arriving in unpopulated terrain, such as onto an island, may establish a permanent population of the species. Calculation of such probabilities is extremely complicated, but meaningful functions of the probabilities can be obtained easily with the mechanical model. If it is desired to determine how frequently a single, adult, pregnant female could be expected to establish a population, the appropriate mortality and reproductive rates can be arranged on the model and then a single "female" ball released on one of the adult fields. The population may "take hold" and build up to equilibrium or it may die out. If the process is repeated many times, a statistically valid ratio of successes to failures can be obtained. The ratio obtained in this manner is not the same as the ratio that would be expected in the wild, however, because the model has no mechanism for preventing uninseminated females from reproducing. In the wild when a population is attempting to establish itself and the numbers are still small, there is a high probability that one or more estrous females might miss one or more breeding seasons because of a total absence of breeding males in the population at the proper time, but on the model a population made up entirely of females would continue to reproduce. Consequently, the proportion of successful colonizations provided by the model would be higher than expected in real life. The error would be comparable, however, in different series of runs designed to compare the effect of different programs of reproduction and mortality on the success of colonization, so the comparisons would remain meaningful.

Two series of colonization tests were carried out under the mortality program used for the runs shown in Fig. 4, beginning with a single adult female. With a reproduction of $3/Y + 2/A$ the population equilibrium oscillates around 26 individuals; the population became firmly established in 10 of 34 trials and died out promptly in the remainder. With reproduction of $4/Y + 4/A$ equilibrium is about 106; the population became established in 11 of 20 trials.

Study of the factors that lead to successful colonization on the model shows that, other factors being equal, establishment of a population is likely to occur more frequently in populations in which the programs of reproduction and mortality lead to population equilibrium at a high level, and in populations that do not fluctuate violently. Important in the stability of these populations are the need that a high proportion of the mortality be compensatory, and that as much of the reproduction as possible be carried out by the younger groups.

AN ALGEBRAIC MODEL

Although the mechanical model was conceived to circumvent mathematics, once the model is thoroughly understood it becomes tempting to analyze step by step the action of the model and to assemble an algebraic imitation of the mechanical model. Table I illustrates the construction of such an algebraic model arranged in a form to make it possible to calculate the number of young and number of adults that will exist in the population at some future time, as well as the level at which population equilibrium will be reached. A few of the expressions provide only an approximation of what the model accomplishes with more precision, but the approximations are close enough so that one is encouraged to experiment with the formula and watch how it handles various problems.

To define completely the dynamics of a population (at least as far as the mechanical model and the formula are concerned), the following facts should be known about the population:

n_{t1}	The number of juveniles in the population at time t1. One can consider the juvenile period to begin either with birth, weaning, or some other stage, and to end either with the first fertile mating, the birth of the first litter, or the weaning of the first litter. One must be consistent, however, and must use mortality rates for the same span.
N_{t1}	The number of adults in the population at time t1, adults being pregnant or parous individuals, depending upon the stage at which one chooses to terminate the juvenile period. Males, regardless of their reproductive condition, are considered to become adults at the same age as females. Note that lower case letters are used for symbols associated with juveniles and capitals for adults.
l	Average size of litters produced by juveniles, exclusive of litters of 0. Litter size at birth or at weaning should be used to match the stage used in defining n_{t1}. If size of litter varies with population density, see bc.
L	Average size of litters produced by adults, exclusive of litters of 0. Same qualifications as listed under l.
♀	Percent of the juvenile population that gives birth. The sex ratio of juveniles as well as sterility, resorption of entire litters, etc., enter into this percentage. Males are not considered to reproduce.

	If the percent of the juvenile population that gives birth varies with population density, see bc.
♀	Percent of adults that gave birth. See comments under ♀.
r	Elapsed time between birth (or weaning) and production (birth or weaning) of the first litter. The symbol stands for the reproduction interval of juveniles.
R	Elapsed time between production of litters by adults (reproduction interval of adults).
dim	Density independent mortality of juveniles, expressed as the constant number of juveniles removed from the population on one unit of area during one r. This is the equivalent of removing by hand a certain number of balls from the juvenile field of the board every fixed time interval.
DIM	Density independent mortality of adults, expressed as the constant number of adults removed from the population on one unit of area during one R. This is the equivalent of removing by hand a certain number of balls from the adult fields of the board every fixed time interval.
pm	Proportional mortality of juveniles, expressed as the percent of juveniles removed in a linearly proportional manner during each r. This is the equivalent of the mortality resulting from balls dropping through the holes in the board without having been bumped by other balls.
PM	Proportional mortality of adults, expressed as the percent of adults removed in a linearly proportional manner during each R. In the formula both pm and PM usually appear as survival rates (1-pm and 1-PM) rather than as mortality rates.
cme	Compensatory mortality exponent for juveniles, representing the extent to which mortality increases, per unit area during one r, as a function of population size. See CME.
CME	Compensatory mortality exponent for adults, representing the extent to which mortality increases, per unit area during one R, as a function of population size. In the absence of meaningful values for this exponent from field data, one must make freehand estimates. In the algebraic formula, the compensatory mortality expression is in the form $-[N - N^{CME}]$. With CME in the form $(Nx + y)$ it is easy to select a pair of exponents that will reduce a population with whatever degree of compensation is desired. If, for example, one wishes to find the compensatory mortality exponent that will reduce during one R a population of 10 to 8 and a population of 100 to 30, then: $10 - 10^{(10x+y)} = 8$ and $100 - 100^{(100x+y)} = 30$ $x = .0069$ and $y = .232$ and the entire compensatory mortality expression will be: $-[N - N^{(.0069N+0.232)}]$ The CME is the $(.0069N + 0.232)$ part of the expression. A less elegant but simpler method is to select some number between 0 and 1 and use it alone as the CME, such as $-[N - N^{0.8}]$. The smaller the exponent the greater the compensation. This is the method I have used in the calculations that follow.
bc	The breeding correction for juveniles. See BC.
BC	The breeding correction for adults. An appropriate breeding correction is used when it is necessary to alter the reproductive rate with changing population density. The most frequently suspected alteration in wild populations is a reduction in reproductive rate as populations increase, and this may express itself as smaller litters or a lower percentage of successfully reproducing females. In the algebraic formula litter size (L) and percent of animals producing litters (♀) appear as a product $L \cdot ♀$, and this product can be modified in several ways by an appropriate BC. For example, it can be multiplied by $N^{(Nx+y)}$ with x and y calculated in the manner illustrated under CME, or more simply by N^x. With the latter expression a negative exponent reduces reproduction when population density increases (compensation). An exponent of —.04 gives greater compensation than —.02. I should expect that in most examples the breeding exponent should be applied only at population densities above a certain critical level. Most simple exponents such as those mentioned above also require that L and ♀ be not the average litter size and average percent of breeders but the average for each of these at that population level at which reproduction is most successful.

The formula in Table I departs somewhat from the mechanical model in that only 2 age groups are carried in the formula instead of 5. The formula could be expanded to include many age groups, but only at the expense of becoming even more unwieldy. Another important difference between formula and model is, as may be seen in Figure 5, the absence of any random fluctuations of population size in the formula. However, when the same population characteristics are fed into the formula and into the machine, good agreement, except for random fluctuation, is obtained.

In Fig. 5 are a series of curves of population growth obtained by introducing the minimum number of young and of adults into the formula in Table I, carrying out the calculations to obtain the population size at one adult generation period later, then repeating the calculations using the new population size, *et seq.* until population equilibrium is reached. By this means it becomes possible to study the effects that changes in mortality and reproduction have on the rate of growth of populations, on the equilibrium size of the population, on the lower limit at which survival can be expected, on the rate of recovery of decimated populations, and on the ratio of young to adults, exactly as with the mechanical model except for the absence of random fluctuations.

In each of the 4 panels in Fig. 5 the center curve represents the growth of a population under

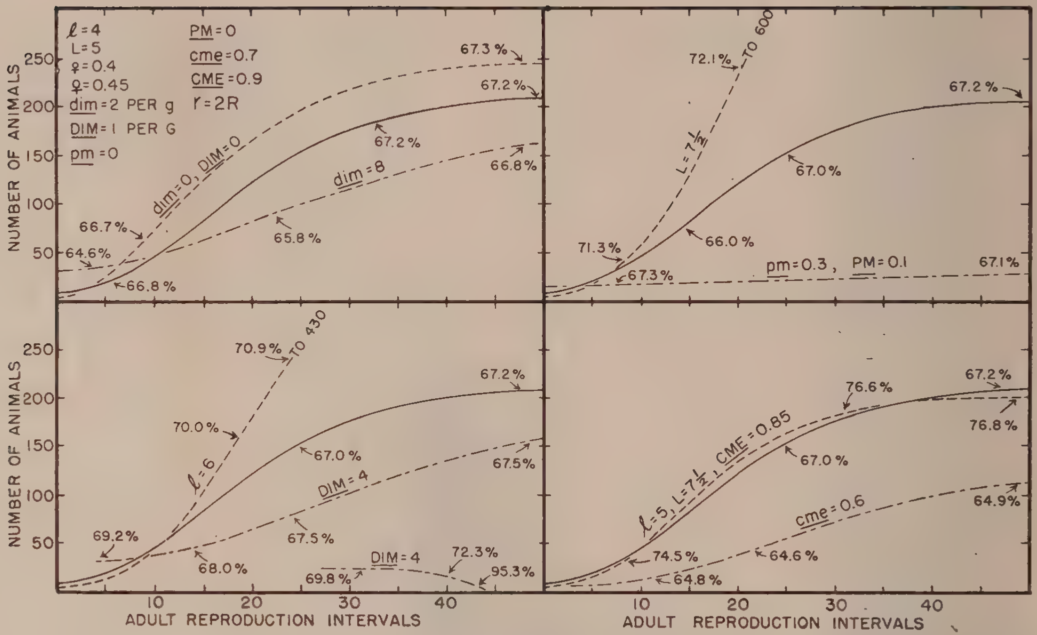

Fig. 5. Changes in the rate of growth, level of equilibrium, and proportion of juveniles in a population when one or more of the mortality and reproduction factors in Table I is altered. The middle curve in each panel represents the population defined by the characteristics listed in the upper left corner; the other curves should be compared with this reference curve.

the following program: $l = 4$, $L = 5$, ♀ = 0.4, ♀ = 0.45, dim = 2, DIM = 1, pm = none, PM = none, cme = 0.7, CME = 0.9, r = 2R, bc = none, and BC = none. This program dictates a high-reproduction, high-mortality, mouse-like population with no proportional mortality on juveniles or adults and with no density-dependent effects on reproduction.

Increasing the density independent mortality on the juveniles by a factor of 4 (dim = 8) raises the population level below which the population will not survive, decreases the rate of growth of the population, and brings the population to equilibrium at a lower level than under the reference program (upper left panel of Fig. 5). A 4-fold increase in density independent mortality on adults (DIM = 4 in lower left panel) has an effect similar to that of increased dim. Extinction of this population when its size has fallen below the lower critical level is also shown. In contrast, when density independent mortality is lifted completely from both juveniles and adults (dim = 0, DIM = 0 in upper left panel), the population can exist at a lower level, grow more rapidly, and reach a higher level at equilibrium.

Addition of some proportional mortality (pm = 0.3, PM = 0.1 in upper right panel) raises the level below which the population cannot recover and lowers the equilibrium level. In fact, this program of reproduction and mortality imposes a surprisingly narrow range of population size within which the population can exist. Were the population to increase for some reason above this range it would quickly return to equilibrium at a level of 20 juveniles and 10 adults. Were the population of juveniles and adults to be cut in half for some reason, the population could not recover. A species characterized by such a program of reproduction and mortality would, therefore, be living precariously near extinction.

When the compensatory mortality on juveniles is increased by lowering the cme from 0.7 to 0.6 (lower right panel), the lower limit of existence is raised, the rate of growth is slowed, and the equilibrium level is lowered just as when the other kinds of mortality are increased. Note in the various curves that although compensatory mortality is what enables the population to come to equilibrium, both proportional mortality and density independent mortality influence the level at which equilibrium is achieved.

Increasing the litter size of juveniles from 4 to 6 (lower left panel) lowers the limit at which the population can exist, increases the rate of growth of the population, and doubles the population level at which the prescribed mortality program imposes equilibrium. When adults bear litters of 7½, instead of 5 as in the reference curves, the population triples before equilibrium is reached (upper right panel).

Any increase in the rate of reproduction of either juveniles or adults causes an increase in the proportion of young in the population (see for example the curves for $l = 6$ in lower left panel and L = 7½ in upper right). Changes in mortality, however, have a more complicated action on the proportion of young to adults. A considerable change in the amount of proportional or density independent mortality on juveniles has only a slight effect on the proportion of juveniles in the population (see various curves in Fig. 5). This is because increased mortality on juveniles prevents them from reaching adulthood, so the decreased number of juveniles is almost matched by a decreased number of adults, causing little change in the ratio of young to adults. Changes in adult mortality under some conditions have a considerable effect on the ratio of young to adults, but under other conditions the effect may be slight. Note in the lower left panel that raising DIM from 1 to 4 only raises the proportion of juveniles at equilibrium from 67.2 to 67.5. Under some conditions it is even possible to *increase* the proportion of adults by killing off more adults.

Because it is not known how much of each kind of the 3 mortalities is operating in wild populations, it is revealing to compare the behavior of the curves in Fig. 5 with the behavior of populations in the wild and to deduce certain facts about the mortality in wild populations. If we think in terms of an isolated population of a mouse such as *Microtus,* a population in equilibrium at a level of 200 or 300 individuals, it becomes clear after experimenting with various mortality programs that no simple exponent for cme and CME provides rapid enough control. Even when *all* mortality is compensatory it takes 20 or more adult generations to approach equilibrium from a low population, whereas in a wild population one would expect at least the potential for more rapid population increase. Consequently, the dynamics of a wild *Microtus* population could be more closely imitated by including a breeding correction (bc and BC) in addition to compensating mortality exponents, or by use of more leveraged compensatory mortality exponents such as $(nx + y)$, or even 2nd power compensatory mortality exponents.

The rate of growth of the reference population in Fig. 5 is clearly not adequate to match the hundreds-fold increase of a population such as the lemmings at Point Barrow, Alaska. The reference curve at its most rapid rate of growth requires more than 7 adult generation periods for doubling of the population whereas lemming populations in the wild can increase faster than this. To approximate more closely the lemming situation, therefore, one must juggle the variables that determine the shape and slope of the curves. The upper curve in the lower right panel of Fig. 5 offers a closer approximation. Litter size of the juveniles was raised from 4 to 5, and of the adults from 5 to 7½, which is closer to the average for female lemmings in the wild (Pitelka 1957), and which provides a steeper growth rate for the population. Compensatory mortality on adults was increased at the same time by lowering CME from 0.9 to 0.85 to keep the equilibrium level at about the same population density as in the reference population. It was surprising to find that an enormous increase in compensatory mortality on juveniles (by lowering cme from 0.7 to 0.3) was necessary to compensate for the greater reproductive rate whereas a small increase in compensatory mortality on adults was more effective and provided a growth rate closer to that of the wild population although still not providing completely for the several-hundred-fold increase shown by lemmings during their 3-year or 4-year cycle. To provide more rapid growth with the same reproductive rate it would be necessary to use one of the more complex compensatory mortality exponents suggested earlier or to combine a lower rate of mortality with a compensatory breeding correction. The ratio of young to adults provided by the lemming curve (upper curve in lower right panel of Fig. 5) appears to be reasonable, but no field data are available for comparison. The ratio of juveniles to adults is one of the most important measurements for understanding the dynamics of a wild population, yet because unweaned young are rarely included in samples, the juvenile/adult ratio is seldom reported for populations of small mammals.

Recovery after catastrophes

Climatic extremes, sporadic invasions by large numbers of predators, and other catastrophes frequently do not kill members of various age classes in proportion to their numbers in the population,

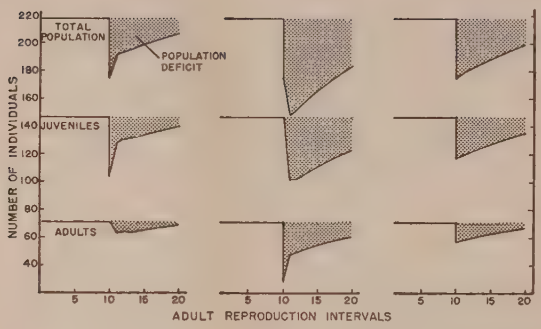

FIG. 6. Effect of removing 44 juveniles (left), 44 adults (center), and 44 juveniles and adults in proportion to their number in the population (right) from a population at equilibrium. The population is the one postulated for the reference curves in Fig. 5.

and the rapidity of recovery of a population from such intermittent mortality depends upon which age classes suffer most of the mortality. If juveniles have small litters, much sterility, a predominantly male sex ratio, and a normally high mortality between birth and littering, then death of a large number of juveniles will not have as serious an effect on the population as death of an equal number of adults. In Figure 6, for example, I have shown the effect of removing 44 animals from the population represented by the reference curve in Fig. 5. The animals are removed from the population when it is at equilibrium at a level of 215 individuals. In the first column 44 juveniles are removed from the population, and it may be seen that the effect on the population is less drastic than when 44 adults are removed (middle column). When the 44 animals are removed from the population in the same ratio as young and old exist in the population (non-selective mortality), then the effect on the population (third column) is intermediate between those produced by the other 2 procedures.

The impact of a catastrophe on the population can be measured by the stippled areas labelled "Population Deficit" in Fig. 6. If the catastrophe is, for example, severe predation, both the prey species and the predator species would probably benefit when the stippled area is minimal. Since non-selective mortality (column 3) is a special case and would rarely provide the minimum population deficit, it seems likely that natural selection has favored the survival of prey species whose behavior exposes the least valuable age class and sex to predation and other causes of death. Similarly, natural selection would favor a predator that modified its habits so that it preyed primarily on the age class and sex least important for the production of a large number of prey.

It is clear from studying the manner in which the formula in Table I functions that a population able to recover rapidly from a catastrophe is not necessarily one that is able to withstand a steady, increased mortality. Similarly, a population that can spare 44 juveniles more easily than 44 adults to some momentary catastrophe might be more quickly exterminated by a small steady loss of juveniles than by the same steady loss of adults.

A low-reproduction, low-mortality population

To contrast with the high-reproduction high-mortality examples used in Fig. 5, a low-reproduction low-mortality example is given in Figure 7. For this example I have extracted the following natural history information from Tables 25 and 32 of Taber and Dasmann (1958) dealing with a population of deer living in 100 square miles of chaparral:

$l = 0.548$ This is the reproductive multiplier for the the juvenile population when the population density is low. The data were not presented in a manner making it possible to calculate l and ♀ separately.

$L = 1.082$ Reproductive multiplier for adult population when the population density is low.

$r = 2$ years Animals are considered to be juveniles up to 2 years of age.

$R = 1$ year Individual females bear young each year.

$\underline{bc} = (n_{tl} + N_{tl})^{-.085}$ The reproductive performance of females declines when the food supply is poor. The same race of deer living on better range nearby were twice as prolific. I have chosen a breeding correction, therefore, that will cut in half the productivity of the females when the population density of the deer reaches equilibrium at the 3448 individuals per 100 square miles reported by Taber and Dasmann.

In the absence of field data on the amount of density independent, proportional, and compensatory mortality, I have set up the following mortality program which when combined with the preceding schedule provides for an equilibrium near the desired 3448 deer per 100 square miles, an age structure of 41.9% juveniles, which is close to that of the wild population, and a maximum rate of growth of the population sufficiently great to permit the most rapid increase shown in Taber and Dasmann's Figure 4:

$\mathrm{dim} = 0$

$\overline{\underline{\mathrm{DIM}}} = 0$

$\mathrm{pm} = 0$

$\overline{\underline{\mathrm{PM}}} = 0.1$ Much of the mortality produced by shooting of adult deer is probably proportional rather than density independent or compensatory.

$\mathrm{cme} = 0.95$

$\overline{\underline{\mathrm{CME}}} = 0.978$

The curves on the left side of Fig. 7 trace the growth of a population with the above character-

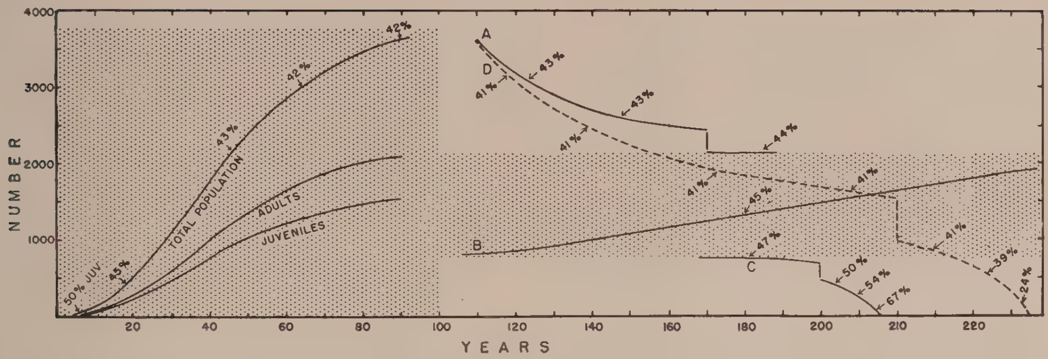

Fig. 7. The 3 curves on the left represent growth to equilibrium at 3820 animals of a hypothetical deer population under the program explained in the text. Curve A represents the reduction of this population to a new equilibrium at 2135 individuals when mortality is increased by removal of 50 additional adults each year. This curve, and others, have been broken to save space. Growth rate of the population under this increased mortality is shown by line B. If the population should drop below the critical level of 748 animals, it would die out in the manner shown by curve C. The stippled area shows for each population the range between the lower critical level and the equilibrium level. Curve D traces the decline of the population to extinction when 50 juveniles instead of 50 adults are removed each year.

istics from low density to equilibrium. They seem to match most of the characteristics of the Taber-Dasmann deer in chaparral and could be used, for example, for estimating the speed of recovery of the population following decimation. Note that as a consequence of low mortality and low reproduction the proportion of juveniles in the population is much lower than in the high-mortality high-reproduction regimes illustrated before. One unsuspected characteristic of the population emerges; the proportion of juveniles is much greater when the population is small. In fact, in populations smaller than 60, juveniles outnumber adults.

One important characteristic of a population is its resilience, and this can be studied by increasing the mortality in different ways and noting the effect on the population. For example, suppose some new mortality factor such as hunting by archers enters the situation and kills 50 adult deer each year in a density independent manner (add $\overline{\text{DIM}} = 50$ per R to the formula). When this is done, the population drops in the manner shown by curve A in Figure 7 and after a century or more would reach a new equilibrium at a population density of 2135 deer per 100 square miles. Fluctuations would of course occur about this new equilibrium level, but if they exceeded 2135 they would be brought back to it, and if they dropped below they would be brought back at the rate shown by curve B. Addition of $\overline{\text{DIM}} = 50$ to the original formula, however, raises enormously the lower critical limit at which the population can exist. If for some reason the population exposed to this additional mortality should fall below 748 individuals, the population would die out in the manner shown by curve C. This population, therefore, can only exist between densities of 748 and 2135 per 100 square miles (the stippled zone in the right hand portion of Fig. 7). Note that the additional mortality of 50 adults per year has little effect on the proportion of juveniles in the population in curve A, but that when the population becomes low (curve C) the proportion of juveniles rises rapidly.

If instead of 50 adult deer the archers are permitted to kill 50 juveniles per year (since the juvenile period lasts 2 years this would enter the formula as $\overline{\text{dim}} = 100$ per r), the population would diminish in the manner shown by curve D. This curve never flattens out and the population becomes extinct after about 200 years. It is surprising that removal of 50 non-reproducing individuals per year has a more severe effect than removal of 50 breeding individuals. This paradox is understandable when one realizes that increasing the mortality between birth and the time of production of the first litter has exactly the same effect on the population as delaying the time of sexual maturity. The formula does not and need not distinguish between these 2 effects. Cole (1954) has already shown how delaying the age of reproduction, even in a species with small litters, can drastically depress the growth of a population because it delays the time at which the compound interest of reproduction begins. By increasing hunter-predation on juveniles, we are doing the same thing as delaying the age of reproduction.

One has the impression that a deer population in equilibrium at a population density of over

3000 per 100 square miles should be able to withstand each year the death of 50 additional juveniles per 100 square miles without becoming extinct. If field evidence becomes available showing that a deer population under these conditions does indeed have a greater resilence than this, then it will be necessary to modify the formula slightly, perhaps by changing the breeding correction or the compensatory mortality exponent, to provide the necessary increase in resilience. Eventually a formula would be obtained that would truly reflect the wild population and that would enable one to predict what effect changes in mortality and reproduction would have on the population. In the case of deer, such a formula could be used to calculate what hunting regime would provide the largest yield of game. Using the present formula the yield at the equilibrium of 3820 deer would be 10% (PM = 0.1) of 2220 adults, or 222 deer. By allowing archers to take 50 additional adults, the population is brought down to 2135 so that conventional hunters now only get 10% of 1203 adults and the total yield would be 50 + 120 = 170.

Summary and Conclusions

A mechanical model is described that is capable of handling numerous variables such as litter sizes of different age groups, sex ratio, density independent mortalities of different age groups, proportional mortalities of different age groups, compensatory mortalities of different age groups, and compensatory alteration of the breeding rate. These variables can be changed singly or in combination to demonstrate what the effect will be on the size of the population at equilibrium, the stability of the population, and the age structure and sex ratio of the population.

In this report examples are given of the size and the fluctuations of a population under fixed, high mortality but under different programs of reproduction. The population was most stable when most of the reproduction was being carried out by the younger age classes. Production of large litters and synchronous (seasonal) breeding made the population highly susceptible to compensatory mortality. The model is also valuable for estimating important parameters that are impossible or very difficult to measure in a wild population, such as the compensatory mortality on a population, and it can be used for problems such as a study of the probability that a species can establish itself successfully in a new area following introduction of one or more individuals.

An algebraic formula is also presented that, except for the absence of random fluctuations in the population, provides a good imitation of the functioning of the machine. The formula demonstrates that, although compensatory mortality brings a population to equilibrium, both proportional mortality and density independent mortality influence the level at which equilibrium is achieved. When breeding data from a high-mortality, high-reproduction population (lemmings) were introduced into the formula, it became clear that much of the mortality on lemmings must be of a compensatory kind, or else there must be considerable compensatory suppression of reproduction. Field data from a low-mortality low-reproduction population (deer) were introduced into the formula and provided estimates of the population size and the yield of game under different programs of hunting. It showed, unexpectedly, that increased mortality on non-breeding juveniles had a more severe effect on the population than an equal increase of mortality on adults.

Perhaps the greatest value of both the mechanical model and the algebraic formula is that they quickly demonstrate that one cannot trust one's own intuitive impressions concerning the dynamics of a population. If an average, unsophisticated ecologist wishes to predict what will be the growth rate, equilibrium level, and age structure of a population when, for example, mortality on the juvenile age class is doubled, his answer arrived at through hunches and general impressions will probably be grossly inaccurate because his unaided mental machinery cannot handle all of the important variables. Biologists have long recognized the limitations of formulas such as the one described above, but have produced nothing better. I believe that proper use of the mechanical model and the equations derived from it can bring the answers of specific population problems into at least the correct order of magnitude, and, equally important, can reveal the intricate interplay of forces that controls a population—an interplay that otherwise goes unappreciated.

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BIOCLIMATIC INFLUENCES ON THE BREEDING MIGRATION OF *TARICHA RIVULARIS*[1]

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The Western Red-bellied Newt, *Taricha rivularis* Twitty, a member of the urodele family Salamandridae, is known only from Sonoma, Mendocino and Humboldt Counties in northwestern California. It is usually characterized as being confined to the redwood belt north of San Francisco; however, it is not necessarily associated with the redwood forests (Myers 1942, Riemer 1958). Among the currently recognized species of *Taricha, T. rivularis* possesses the most restricted distribution and in many ways is the most specialized and advanced member of the genus (Riemer *ibid.*). This species spends the dry summer underground on land from where the individuals emerge following the onset of the fall rains. During the late fall and early winter they move about on the surface during periods of rainfall and in the evening. Beginning in late January their movements become less random, and some begin to move toward the stream. The magnitude of the migration increases until it reaches its peak in early March. Following breeding, which runs through most of March and into April or later if earlier conditions are unfavorable, the salamanders typically all leave the water wthin a period of a few days and are not found on the surface again until the following fall.

As in other amphibians that exhibit similar behavior, 2 types of factors must be considered as influencing the migration of *Taricha rivularis* to the breeding site. One is the cyclic development of the gonads under the hormonal control of the anterior lobe of the pituitary gland, as has been shown by Rugh (1935a, 1935b, 1937, 1939 and other papers) and others, but an analysis of endocrine relations is beyond the scope of this study. Secondly, being coldblooded and subject to desiccation, these newts may be influenced greatly in their surface activity by the climatic factors of their environment. In this paper the influence of rainfall, temperature, relative humidity and barometric pressure will be examined.

The Study Area

The work was performed on the Hedgpeth Ranch located in the coastal hills west-northwest of Healdsburg, Sonoma County, California. On this property Pepperwood Creek, a tributary of the Wheatfield Fork of the Gualala River, supports a large breeding population of *Taricha rivularis*. A section of this creek, shown diagrammatically in Figure 1, and the surrounding hills were used for the study. The valley floor at this point is at an elevation of about 600 feet. The hills along the south side of the stream are heavily wooded and rise sharply to an elevation of about 1900 feet, while the other bank is bordered by a flat valley floor which then rises to around 1000 feet and is covered with open grazing land and scattered stands of trees.

The stream banks and the north-facing slope are littered with many fallen trees and branches. This litter provides shelter for a variety of amphibians in addition to *T. rivularis,* including the sympatric species, *T. granulosa.*

Materials and Methods

Since the objective of the study was to ascertain the influence of climatic factors on both the magnitude and direction of movement, a system of traps was constructed in order to obtain more consistent samples for corparison than could be obtained by visual observation and manual collection. These traps were a modification of the design used by Fitch (1951), Storm and Pimentel (1954) and others, and consisted of a rectangular cage into which animals were funneled by long arms or drift fences. They were constructed of a flexible grade of one-quarter inch mesh hardware cloth.

In an effort to capture as many animals as possible during their movement in a certain area, the cages were arranged in series. One series (see Fig. 1), consisting of 10 cages and their connecting drift fences, ran along the south side of

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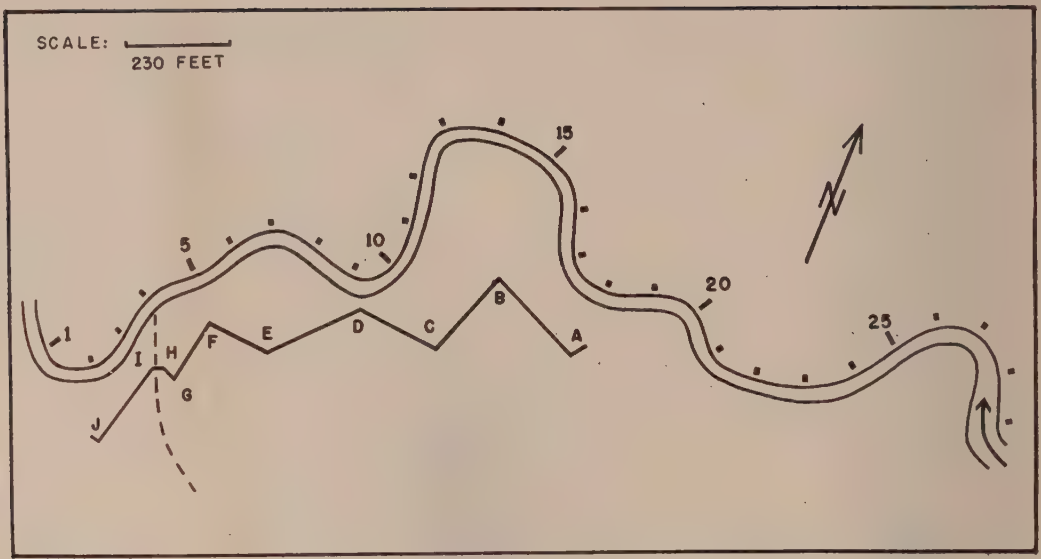

Fig. 1. Map showing the study area of Pepperwood Creek and the relation to it of the stream-side trap series (A to J).

the stream at the base of the hills. It covered about 250 yards of actual stream length and was located from 5 to 150 feet from the stream bed depending upon topography. The 2nd series, consisting of only 3 cages, was located in a small clearing on the hillside about 750 feet from the stream and 200 vertical feet above the lower series.

In an effort to establish more closely the time of movement, traps A, B, D and E shown on Fig. 1 were modified, and switch mechanisms were installed during the last season of work. These consisted of a rocker plate upon which the animal fell after leaving the entrance funnel and which in turn briefly closed a microswitch connected to a recording instrument.

Another group of traps, constructed in the fall of 1957, consisted of circular fences surrounding the bases of Pepperwood trees (*Umbellularia californica*) and attached to funnels and cages as described above. These traps, 3 in number, were designed to capture animals emerging from subterranean passages at the bases of these trees. Two of them were located near the hillside trap series and the 3rd on the other side of the creek about 25 feet from the water.

All climatological data used in this report were collected at the study site. All of the instruments were portable and easily maintained in the field. The microswitch system and the aspiration of the hygrothermographs were powered by dry cell batteries.

Several hundred animals were toe-clipped for individual recognition, and their movements will be reported in another paper.

RESULTS

Precipitation

As mentioned earlier, *Taricha rivularis* spends the dry summer period underground, and animals do not appear on the surface until after the fall rains have begun. During the period of the study, 1956 through 1959, they did not emerge until after several rains, unlike *T. torosa* studied by Stebbins (1954) which emerged after the first rain. Table I shows the date of the first trap capture of animals of the season, the amount of rain which fell during that 24 hour period, the total precipitation prior to that day since the summer dry period and the total rain for the season. It can be seen from the table that there is no correlation between emergence and either the amount of rain concurrent with the first capture, the amount preceding that date or the cumulative total for the season. Clearly the animals that emerged in October 1956 did so after a violent storm, but this was not so in the other years, and it would appear that violence of precipitation is not necessarily a factor in emergence.

These figures suggest that as the season advances less and less rainfall is required for emergence, but whether rain or any other factor acts as a stimulus or only passively permits surface activity is not known. It appears likely, since emergence is the first visible manifestation of

TABLE I. The relation of rainfall to the first capture of animals for the season

Date of first capture	Total rain of storm concurrent with emergence (inches)	Total rain before storm concurrent with emergence (inches)	Season total to date (inches)
10-30-56	4.04	1.69	5.73
10- 5-57	0.50	6.38	6.88
11-18-58	0.82	0.73	1.55

reproductive behavior, that innately controlled hormone activity is the primary factor causing emergence and that as this breeding drive increases the animals can emerge under drier conditions. The physiological condition of the animals during the summer is not known, *i.e.*, whether or not the animals are estivating. They must, however, be in a good physiological state since gamete formation takes place in large part during the summer period, apparently including some yolk deposition. This has been clearly shown by Miller and Robbins (1954) in *T. torosa* and the same appears to be true in *T. rivularis*.

These early emergents were few, and additional individuals continued to emerge for some months. During the 1957-58 season, when selected trees were circled by traps, it was found that after almost every rain additional animals were captured until the middle of February. Whether this difference is due to diverse summer niches or to individual physiologic differences is unknown.

From February through the remainder of the breeding season, rain has a profound effect on both the magnitude and direction of movement. This is shown by comparing the numbers of animals captured in the series of traps which ran along the foot of the hillside beside the stream with the total precipitation for the preceding 24 hours. The rainfall figures used throughout this paper are for the 24-hour period ending at 1030 hours (10:30 AM) since this was approximately the time the traps were checked. In all cases where a date is given it represents not a calendar day but a "salamander" day ending at 1030 hours on that date.

Table II shows the correlation between the number of animals moving toward the stream as measured by trap captures and various classes of rainfall for the 1956-57 and 1957-58 seasons combined. These rainfall classes are arbitrary divisions but nevertheless reflect different types of precipitation from light drizzles to heavy downpours. The captures on days with no rain showed extreme variation, from one day with no animals to one with 108. Usually, increasing rainfall decreased the number of animals caught while moving toward the water.

TABLE II. The relationship between rainfall and the magnitude of capture of animals moving toward the stream for the 1957 and 1958 seasons combined

Number captured	DAILY RAINFALL (inches)				
	None	Trace 0.15	0.16- 0.75	0.76- 1.50	1.51+
0	1				2
1-10	28	4	7	3	4
11-20	7	3	7		
21-30	4	1		1	
31-40	1	3	1	2	
41-50	4	1		1	
51-75	2			1	
76+	2				

Table III, which compares the same rainfall classes with the movement away from the stream, shows an entirely different picture. In this case the greater the rainfall the greater the capture. It should be pointed out here that both of these tables cover only the periods of the migration to the breeding site and breeding itself and do not include the return movement at the end of the season.

TABLE III. The relationship between rainfall and the magnitude of capture of animals moving away from the stream for the 1957 and 1958 seasons combined

Number captured	DAILY RAINFALL (inches)				
	None	Trace 0.15	0.16- 0.75	0.76- 1.50	1.51+
0	32	2	4		
1- 5	16	7	10	1	1
6-10		1		2	2
11-20			1	2	3
21-30				2	
31+				1	

In both of these tables the days following the general trend are enclosed by a heavy line. There are, however, apparent exceptions to these trends. A further analysis of these exceptional days reveals some of the modifying influences. For example, a light continuous rain, even if great in total amount, had a less profound effect than the same amount falling in a short time. Also, the effect of a given amount of precipitation depended in large measure on both the rainfall and the temperature of the preceding day or days; frequently more animals than expected were captured moving toward the water on days following an inch or more of rain while fewer than expected were captured moving away from the stream. On days of roughly equal rainfall, more animals were captured moving toward the stream when the temperature was relatively high than when it was lower. The time of the rain was important also; higher captures than expected were recorded upon occasions when rainfall began after the migration toward the stream was underway.

Movement out of and away from the stream during the breeding season and the character of the stream were correlated. An increase in stream volume from that of the previous day of as little as 2 cubic feet per second, as measured by a velocity-head rod (Wilm and Storey 1944), was reflected in an increased capture in the traps. Stream volume changes are, of course, directly dependent upon rainfall and would influence only those animals already in the water. Associated with increased volume, however, was increased sediment load. Several times during the 1959 season a very light rain fell which did not influence the volume but did increase the amount of particulate matter in the stream. On these occasions animals were less numerous in the water although they did not move far enough away to be captured in the traps.

Thus rainfall can account in large measure for many of the differences in the observed number of animals which were trapped from day to day while moving toward the stream, and it apparently accounts entirely for changes in direction of movement, that is, movement away from the water during the period of the breeding migration. Variations in the magnitude of capture on days when there was no precipitation remain to be explained, but before the rôle of other environmental factors can be discussed in this regard, some information on the time of movement must be presented.

The microswitch system which was installed in 4 of the traps proved quite effective in recording the time animals entered these traps, since it gave a time resolution of separate captures down to about one minute. Movement toward the stream was not uniform through the day but occurred primarily at night. Moreover, the 5 peak hours, 1700 to 2100 hours, were early in the evening beginning roughly at sunset. I say "roughly," since the study area became completely shaded approximately an hour before the time of the true sunset. The smallest number of captures occurred during the early morning. Considering the season as a whole, movement away from the water was much more evenly distributed through the day than was the movement toward the stream.

In addition to these differences in the time of capture through the season, a difference between traps was found. Among the traps capturing animals moving toward the stream, a significantly smaller proportion of the total was captured in Trap D (see Fig. 1) than in the others, in the ratio of approximately 1 to 5 during the early part of the season, *i.e.*, up to February 24th. The only major observable difference between Trap D and the others was its location in relation to the stream. It was situated, depending upon the stream volume, 3-5 feet from the water's edge while the others were 50 to 75 feet from the nearest point of the stream. Since traps B, D and F were approximately in a straight line, these results appear to indicate that the animals either "knew" the location of the stream or were able to "detect" its proximity and did not approach it closely until either the animal or the stream was in condition "suitable" for breeding.

Since the bulk of the migration occurred at night, a comparison was made of the time of capture and its daily variation with the phases of the moon and the time the moon was above the horizon, but no correlation was found.

The basis for using 1030 hours as the beginning of the day has already been discussed. In the following sections on the role of temperature and relative humidity, mean values for these factors for the 8-hour period from 1800 to 0100 hours are used. This is the middle ⅓ of the "salamander" day, and, while it does not include all of the peak capture hours, it was selected as a typical measure of conditions met by the animals during the period of their surface activity.

Temperature

The role of temperature in the emergence of *Taricha rivularis* from underground in the fall and winter is unknown. No consistent records were made during the fall months; however, the general temperature trend was downward. This is in contrast to the effect of increasing air temperature which is stressed in the emergence of several urodele species, for example *Ambystoma maculatum* (Wright and Allen 1909, Piersol 1929), *A. texanum* (Smith 1934), *A. jeffersonianum* (Bishop 1941) and *Hemidactylium scutatum* (Blanchard 1934, see also Bishop 1943:309) as well as in a number of anurans. These species, however, hibernate during the winter and emerge in the early spring to breed. Further studies of the temperature, particularly of the ground at the depth at which the animals spend the summer, are required before its role in this regard can be established for *T. rivularis*.

During the breeding migration, especially at its height, which was roughly the first three weeks of March in 1957 and 1958, temperature appeared to play an important role. The importance of "mild temperatures" or "warm days" also has been stressed for the surface activities of *Ensatina eschscholtzi* (Stebbins 1954), *Notophthalmus* (=*Diemictylus*) *viridescens* (Morgan 1939) and *Taricha granulosa* (Chandler 1918).

The time-of-capture records for 1958, which were recorded as the number captured in the 60 minutes preceding the hourly interval, enables us to know quite closely the actual temperature at the time the animals entered the traps. The mean temperature at the time of capture of animals moving toward the stream was 48°F and it was 50.4°F for those moving away. These means are statistically different from each other ($P. < .05$) on the basis of "Student's" t-test, but the higher temperature associated with movement away from the stream was probably attendant on rainfall and therefore not of primary importance.

A further analysis of these data was made by comparing the mean temperatures for the period 1800 to 0100 hours on the days of largest capture of animals in all of the traps measuring movement toward the stream with those of the days with smallest capture. The means were not significantly different. This is not surprising since other factors, particularly rain, were disregarded. If we compare only means from days when it did not rain a different picture is found. In this case the mean temperature for these hours on nights of high capture was 44.1°F, which is significantly greater than that on nights of low capture when the mean was 40.9°F.

When the same comparisons were made for the preceding year, 1957, different statistical results were obtained. When all days were used, irrespective of rain, there was a statistical difference between the means, but none when only the days with no rain were studied. Although not significantly different, in 1957 the mean temperature on nights of high capture when there was no rain was higher than on nights of low capture, 50.6°F and 47.1°F, respectively. The difference between these means is greater than that between the comparable figures for 1958, but the variance also is greater.

Probably not too much emphasis should be placed on these statistical comparisons. In the "t-test" used to compare the means, only 6 to 11 items were employed in each class since this was all that were available in the brief period of animal activity each season when the middle values were eliminated and only the extremes of capture compared. It was not possible to combine the data for the 2 years to obtain larger classes since the temperature regimes were quite different. In addition, there was variation in the number of animals "available" to respond on consecutive days and in the unmeasured influence of the physiological, particularly hormonal, state of the animals.

This relationship between temperature and the magnitude of capture is illustrated for the 1957 season in Figure 2. A close correspondence can be seen in the nature of the curve for the mean temperature for the period 1800 to 0100 hours (dotted line) and the histogram showing animals captured moving toward the stream. This relationship breaks down during the latter part of the season after the peak of the migration; nevertheless, it is quite clear during the period of the major portion of the migration.

A similar study on the relation of temperature to movement away from the stream was made. No correlations were found except ones more readily related to rainfall and its effect upon the daily temperature fluctuations.

During the latter part of the 1956 season and throughout the 1957 season, a second hygrothermograph was in operation almost directly uphill from the one beside the stream. Readings from the 2 instruments were compared with each other and with animal capture in both trap series but no correlation could be found in differences existing between the temperature measurements and the magnitude of capture. If animals did respond to differences in either temperature or relative humidity between the stations, it was masked by daily variations in these or other factors.

Despite these apparent contradictions, it is clear that temperature does influence the number of animals migrating on any specific day, at least as measured by captures in the traps. No pre-season temperature records were kept at the study site to enable us to compare the general temperature pictures for the 2 years, and the nearest stations from which records are available are on the inland side of the coastal hills in a very different ecological situation. However, a comparison of the temperature means for 1800 to 0100 hours during the 2 seasons reveals that the seasonal average for these hours for 1957 was 50.1°F, which is significantly higher than the mean for the comparable data, 44.9°F, for the 1958 season. These figures and the similarity of the correspondence between the temperature curve and the histogram showing the number of animals captured moving toward the stream in both years (see Fig. 2 for

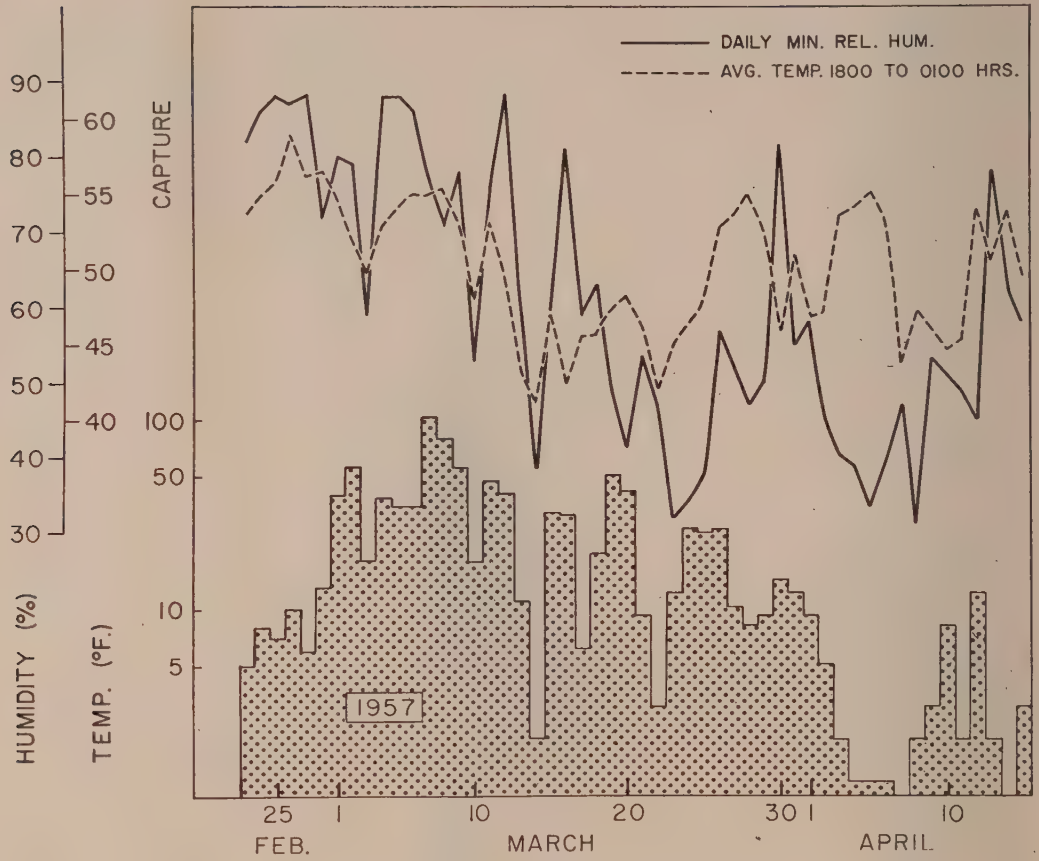

Fig. 2. The relation of temperature and minimum relative humidity to the capture of animals moving toward the stream.

1957 data) lends support to the hypothesis that the influence of temperature is based on its daily variations in relation to the long term trend and the temperatures to which the animals have been exposed during the preceding months. This is particularly true in the early part of the breeding season although the picture apparently breaks down later when fewer animals are still on land.

During the 1956 and 1957 breeding seasons, continuous recordings were made of the stream temperature. No correlation was found, however, with the number of animals observed in the stream.

Humidity

All amphibians are dependent upon water. Most of them require it for reproduction and for the subsequent development of the egg and the larva until metamorphosis. Beyond this, moisture is required to prevent desiccation when the animal is on land. Even completely terrestrial forms must have access to water in addition to that which is obtained in food, and this water must be obtained through the skin since no amphibian is known that can drink.

One possible source of this water is from atmospheric moisture. In the present study this was measured and recorded as relative humidity by the hygrothermograph instruments. A comparison of means of relative humidity from nights of high capture as opposed to low capture in 1957 and 1958 produced negative results and spurious correlations. All of the means compared in these classes exceeded 88% and all but 2 exceeded 91% This, of course, reflects the fact that the maximum relative humidity was usually reached at between 1700 and 1900 hours and stayed at that level except on windy nights through 0900 hours the following morning. Moreover, while the temperature readings at the time of capture in traps B and D formed a rather flat-topped but fairly normal distribution curve, a comparable graph for the humidity data formed an extremely one-sided curve. The mean was 89.3% with a range from 42% to 95%, the maximum recorded on the instrument. A measure of this skewness is shown by the fact that 253, or 77.5%, of the 334 measurements had values equal to or greater than the mean.

Estimates were made of the absolute humidity, calculated from tables (Marvin 1941) for the means of temperature and relative humidity for the period 1800 to 0100 hours. However, since the relative humidity was typically uniformly high during these hours, a curve plotted from these data approximated the one for temperature for these same hours. It appears, therefore, that the amount of water vapor in the air, at least during this period, was without influence on the number of animals moving on any particular night.

The only humidity value which underwent major daily fluctuations was the minimum relative humidity, which usually occurred between 1400 and 1600 hours. When these values were plotted only a rather vague resemblance to the magnitude of capture of animals moving toward the stream was found. However, when daily changes in these humidity values and in the mean temperature for the period 1800 to 0100 hours were compared together with the number of animals captured in the traps, a more definite relationship was found. A cursory examination of the 1957 data, shown in Fig. 2, suggested the following generalizations on this relationship: (1) when both the mean temperature and the minimum humidity decreased in relation to the values of the previous day, capture decreased, (2) when they both increased, capture increased, (3) when the mean temperature decreased but the minimum humidity increased, capture may or may not have increased but did not drop significantly, (4) when the mean temperature increased but the minimum humidity decreased, capture decreased. A closer examination of each day showed that while (1) and (2) held up quite well (3) and (4) did not. Most of the days which did not fit this scheme were ones on which there was little if any change in one or both of the variables. When only those days on which a change from the previous one of 1°F and 3% relative humidity or more occurred were selected, this relationship held up on 25 of the 30 possible days. The same general picture held true for the 1958 season.

The apparent exceptions to these generalizations can be understood by a closer examination of these days and those immediately preceding. Exceptions occurred when an increase in the mean temperature after a particularly cold night apparently overshadowed the effect of a drop in the minimum relative humidity and capture increased. This was probably due to the fact that on such occasions those animals physiologically "ready" to move on that night were supplemented by some which were previously "ready" but inhibited in their migration by the low temperature on the previous night. Rain also modified the picture; heavy rain inhibited movement while, on the day after a heavy rain, regardless of temperature or humidity, more animals than expected were often captured. These apparently included the normal day's quota and those inhibited the preceding day. It is also possible that favorable conditions may have "triggered-off" movement which, once initiated, might continue irrespective of subsequent unfavorable conditions. Such an occurrence would not show up in the average values plotted in the figure.

The manner in which the minimum relative humidity during the afternoon influenced the magnitude of movement occurring at night is not known. It may be due either directly to the amount of desiccation experienced by the animal during the day and the subsequent hydration required before the animal would migrate, or indirectly to this cause and its relation to the location and/or depth at which the animal sought shelter during the day.

A 4th environmental factor which was examined for its possible influence on migration was barometric pressure. No correlation was found, however, between either changes in pressure or the amount of pressure and the magnitude or direction of movement other than those which can more easily and more precisely be defined upon the basis of rainfall alone.

Return to Land

Thus far we have discussed only the period from the time the animals emerged in the fall through the time of egg deposition. The final event of the breeding season is the return of the animals to land.

During the 1956 and 1957 seasons this return leg of the migration occurred concurrently with rainfall in the middle of April. The animals all left the water in from 2 to 4 days, moved uphill, and could subsequently not be found anywhere on the surface or under litter. In 1958 the breeding season was interrupted on March 20 by rain which continued during 14 of the next 17 days. Not until April 7 was breeding activity resumed. There was no more rain from then until May 12 and none of any great amount until June 2. Apparently as a consequence, there was no mass movement out of and away from the stream, but animals were found in small numbers in all of the traps through May 24 when the survey was discontinued. This lack of rainfall in the latter half of April of 1958 was unusual. An examination of U. S. Weather Bureau records (Annual Summary for California) for the 10 year period 1949 to 1958 shows that there was rain on or after April 13 in each case.

It appears that at the end of the 1958 season the animals not only left the water over an extended period but did not move as far from the stream as usual. During the fall and winter of the following season fewer individuals than in previous years were found more than 500 feet from the stream.

Discussion and Conclusions

On the basis of these observations, the relationship between the breeding migration and bioclimatology during the breeding season in *Taricha rivularis* may be generalized as follows: Movement away from the water during both legs of the migration was influenced primarily by rain irrespective of temperature or other factors. Rain also strongly influenced the movement toward the water when in heavy amounts it acted as an inhibitor. On days with no rainfall the magnitude of the migration can be correlated with daily changes in the mean evening temperature and the daily minimum relative humidity. This correlation was not with variation about a fixed mean or range but rather with variations in the values from those of the previous day in relation to the seasonal trend. This was particularly well shown with regard to temperature. In both 1957 and 1958 the mean temperature on nights of large capture was higher than on nights of small capture, but in 1957 the mean temperature of small capture, 47.1°F, was higher than the 1958 mean temperature of large capture, 44.1°F.

Mean evening temperature seems to be more important than daily minimum relative humidity, but a high minimum relative humidity can overcome the inhibitory effect of a drop in temperature as long as the drop is not too great or to too low a point. The mechanism whereby minimum relative humidity in the early afternoon affects the magnitude of migration occurring that night is not clear, but it may be that in response to decreasing humidity the animals retreat farther from the surface and that there is a time lag in their response to increasing humidity at the time of sunset.

This apparent inhibitory effect of a temperature decrease in relation to the general temperature trend of the previous weeks is what might be expected in a cold-blooded animal. Such a relationship in anurans has been repeatedly pointed out by Bragg (1940, 1945), Bragg and Smith (1942), Stebbins (1951) and others.

The ability of amphibians to detect changes or gradients in relative humidity and to respond to them has been shown by Goldsmith (1924-25) and Shelford (1941). Ray (1958) and others have investigated experimentally desiccation in urodeles but their procedures and results do not aid in interpreting field observations such as these.

Noble (1931) and others have proposed that migration may take place without external stimulation in some species. Noble points out that some amphibians retain their normal periodicity of egg laying in the laboratory and "probably, therefore, in their desire to migrate." Whether environmental conditions actually stimulate migration in *T. rivularis* or merely "permit" its occurrence after adequate innately controlled internal stimulation by hormones from the endocrine glands is not clear. This would have to be tested experimentally under conditions other than those employed in this study.

The only generalization that can be made at present is that cyclic changes in the pituitary, affecting seasonal hypertrophy of the gonads (see Rugh 1935a and subsequent papers, Chadwick 1940, Miller and Robbins 1954 and 1955), in conjunction with climatic conditions of which rainfall and temperature seem to be the most important, control the breeding migration of *Taricha rivularis*.

Summary

The influence of bioclimatic factors on the breeding migration was studied in a population of the newt, *Taricha rivularis,* in Pepperwood Creek and the surrounding area in the coastal hills of Sonoma County, California. Results of the study are as follows:

(1) Animals emerge from underground following moderate rains in the fall and continue to emerge at times of rainfall through mid-winter. As the season progresses less cumulative rainfall apparently is necessary before emergence.

(2) Movements away from the stream during both legs of the migration are stimulated primarily by rain independently of other factors, but rain in heavy amounts inhibits movement toward the stream.

(3) In the absence of rainfall the magnitude of

the breeding migration can be correlated with changes in the mean evening temperature (1800 to 0100 hours) and the daily minimum relative humidity from the values of the preceding day. Of the 2, temperature is the more important but a high minimum relative humidity can overcome the inhibitory effect of a drop in temperature.

(4) No correlation was found between either changes in or the absolute level of barometric pressure and the magnitude or direction of movement other than those which can more easily and more precisely be defined on the basis of rainfall alone.

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THE ECOLOGY OF GAMBEL'S QUAIL IN NEVADA AND THE ARID SOUTHWEST[1]

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Introduction

Gambel's Quail (*Lophortyx gambellii*) is the only resident upland game bird native to and abundant on many of the desert areas of the southwestern United States. State conservation agencies responsible for game management on these deserts have turned to this species as the best possibility for providing huntable small game populations in the face of rapidly expanding human populations in these areas, and the consequent demand for recreational opportunities.

This paper reports the results of a detailed study of the habitat requirements of Gambel's Quail on the portions of the Mohave Desert lying within Nevada. The study followed the completion of a water development project, during which a few natural springs were rehabilitated for game use, and 65 gallinaceous guzzlers (*cf.* Glading 1943) were constructed. Included in this study program was an investigation of guzzler usage by Gambel's Quail, and other small game species, and an evaluation of the guzzler as a management technique for increasing small game populations in the arid regions of Nevada. In addition, the general ecology of this quail throughout the American southwest was reviewed.

Distribution of Gambel's Quail

Natural distribution

Gambel's Quail are presently found in the valley of the Rio Grande as far east as the Chisos Mountains in Texas (Moore *in litt.*); then westerly in New Mexico, where they occur "in the valley and drainages of the Rio Grande north to north-central New Mexico [Sandoval County] and southwesterly in the valleys of the Gila, Mimbres, and San Francisco Rivers and their tributaries" and "along both sides of the Organ-San Andres chain of mountains" (Campbell and Lee 1953); across southern and central Arizona south of "A line drawn diagonally across the State, from Clifton near the New Mexico border to Boulder [Hoover] Dam on the northwest boundary . . .," and in scattered localities north of this line (Griner *et al.* 1942); the Virgin River drainages in northwestern Arizona and southwestern Utah as far northeast as Pintura and Springdale, Utah (Greenhalgh *in litt.* 1955); southern Nevada north to Panaca, Hiko and Beatty; and the Mohave and Colorado Desert portions of California north to Death Valley and Mojave and west to Victorville and Banning (Grinnell and Miller 1944); then southerly to northeastern Baja California, Tiburon Island, and to the Rio Culiacan, Sinaloa, on the Mexican mainland (Friedmann *et al.* 1950) (Figure 1).

In Colorado, Gambel's Quail occur in the McElmo Creek Valley, along the lower reaches of the Animas River Valley, and along "Kannah Creek and the Grand Valley area in the vicinity of Grand Junction, Mesa County, and in the area west of Eckert, Delta County" (Sandfort *in litt.* 1956).

However, the origin of these birds in southwestern Colorado is subject to some uncertainty. Bent (1932) said, "There is no definite record of the natural occurrence of Gambel's quail anywhere in Colorado," and he believed this species to be an exotic in Colorado, being brought in from California between 1885 and 1889. Greenhalgh (*in litt.* 1956) and Sandfort (*in litt.* 1956) both have additional information concerning the transplanting of substantial numbers of Gambel's Quail to Colorado and eastern Utah beginning about 1890.

On the other hand, the committee preparing the 1957 edition of the A.O.U. check-list regarded the birds in Colorado as natives (A.O.U. 1957), believing that too little time had elapsed since the supposed original introductions to permit the development of the plumage characteristics which now separate these birds from the typical form. Mearns (1914) first recognized these quail in

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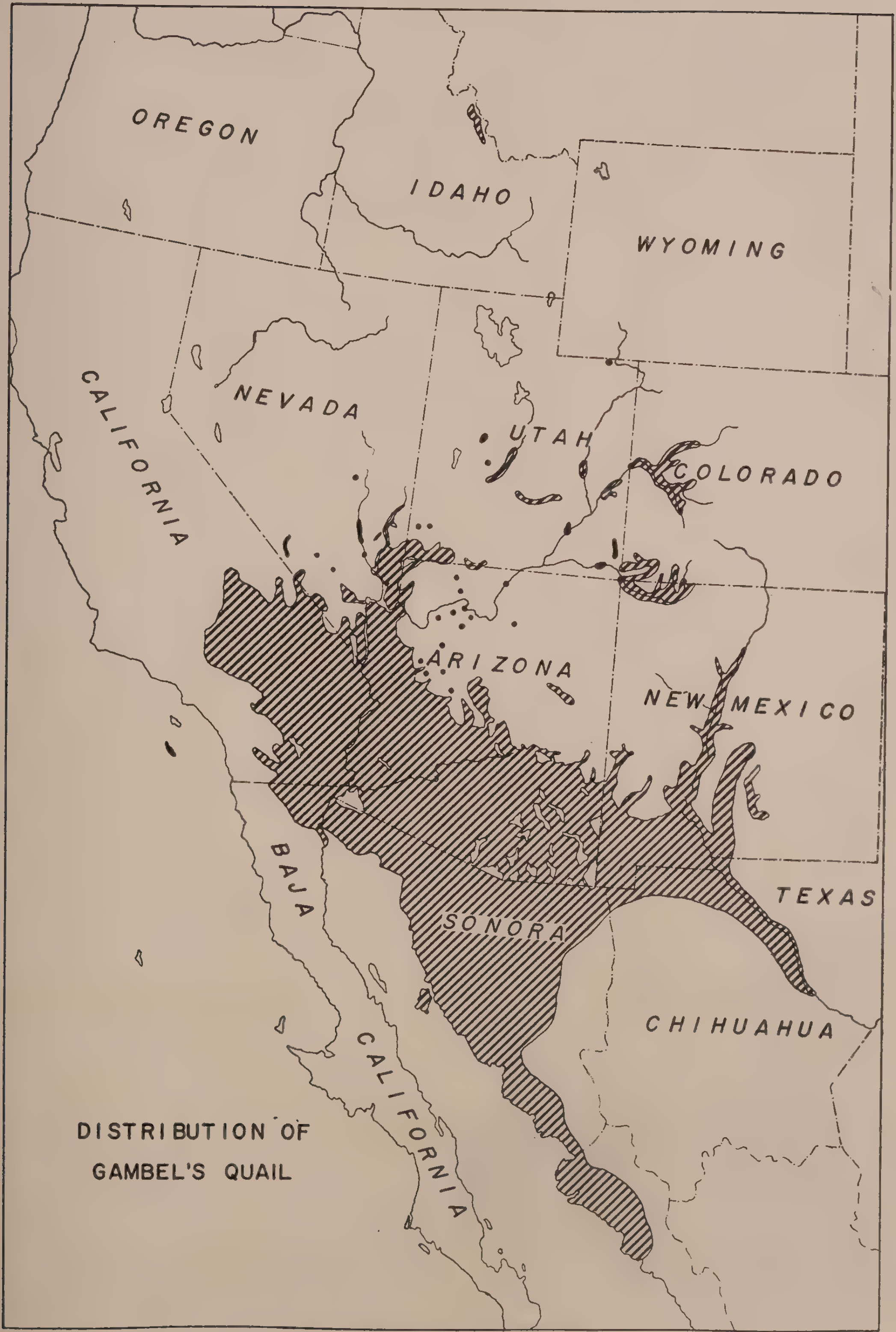
OREGON
IDAHO
WYOMING
NEVADA
UTAH
COLORADO
CALIFORNIA
ARIZONA
NEW MEXICO
TEXAS
SONORA
BAJA CALIFORNIA
CHIHUAHUA
DISTRIBUTION OF GAMBEL'S QUAIL

FIG. 1. The distribution of Gambel's Quail.

TABLE I. Records of successful extralimital introductions of Gambel's Quail

Locality of establishment	Source of stock	Number of birds released	Period of release	Reference
CALIFORNIA—San Clemente Island	?	?	?	Grinnell & Miller 1944
HAWAII—Kahoolawe Island	?	?	?	A. O. U., 1957
IDAHO—Lemhi Valley	Las Vegas, Nevada	?	1919-1921	Anon. 1953
NEW MEXICO—San Juan Valley	?	48	1909	Ligon 1927
Sacramento Mtns, Mora River Valley, upper Canadian River Valley, and upper Rio Grande Valley.	?	?	?	Campbell & Lee 1953
UTAH—Delta, Meadow, Sevier River Valley from Sevier to Gunnison, Newcastle-Enterprise area, Kanab, Fremont River Valley from Loa to Hanksville, Greenriver-Elgin area, Manila, Moab-Dewey area, Hite, Bluff, and Montezuma Creek Valley.	Probably "lower" Arizona and southwestern Utah	?	from prior to 1897 to at least 1914	Greenhalgh *in litt.* 1956
COLORADO—Uncompahgre, Gunnison, and Colorado River Valleys	Southern California "lower" Arizona	"about 1,000" ?	1885-1889 ?	Bent 1932 Greenhalgh *in litt.* 1956
NEVADA—Ursine-Rose Valley area	Overton, Nevada	2 pairs	about 1900	Present study

Colorado as being distinct from the nominate race in specimens collected in 1912, or some 27 years after the first supposed introductions were made.

Racial Distribution

According to Ridgway and Friedmann (1946) and the A.O.U. (1957) the race *L. g. gambelii* (Western Gambel's Quail) is a resident of southwestern Utah, Nevada, California, Arizona, southwestern New Mexico, and northern Mexico (in extreme northwestern Chihuahua and northeastern Baja California south to central Sonora). The quail in southwestern Colorado and northwestern New Mexico belong to the race *L. g. sanus* (Olathe Gambel's Quail); those along the Rio Grande in southern New Mexico and in Texas belong to the race *L. g. ignoscens* (Texas Gambel's Quail); while in southern Sonora and northern Sinaloa, Mexico, *L. g. fulvipectus,* the Fulvous-breasted Quail, is resident; and *L. g. pembertoni* inhabits Tiburon Island, in the Gulf of California.

The recent distributional paper by Aldrich and Duvall (1955) gives a somewhat more restricted range for *gambelii* and a more extensive range for *sanus* than that given by Ridgway and Friedmann and the A.O.U. check-list. Aldrich and Duvall place all of the Colorado Basin portions of Utah as well as the eastern third of Arizona and most of New Mexico in the range of *sanus,* and restrict *gambelii* to western and central Arizona, southwestern Utah, Nevada, California, and Sonora, Mexico.

From the standpoint of climatic tolerances and preferred habitats, as discussed later, it appears that the ecological distribution is best considered on the basis of the racial distributions delineated by Ridgway and Friedmann and the A.O.U. check-list. There appears to be a great deal of difference between the climatic tolerances of the Gambel's Quail in Colorado and those in eastern Arizona and southwestern New Mexico. In addition, there is a considerable extent of hostile and unoccupied range between the major populations of *sanus* in Colorado and the Gambel's Quail farther south. Utah populations in the Colorado Basin, although shown to be continuous by Aldrich and Duvall (1955), are noted by Greenhalgh (*in litt.* 1955) as being very small and isolated populations (Fig. 1). Also, many of these populations are the result of comparatively recent transplants, primarily from *gambelii* populations in southwestern Utah (Table I).

Extralimital Distribution

In the never-ceasing quest for a better game bird, Gambel's Quail have been transplanted by sportsmens groups, and others, into many extralimital areas. Although failures have been more frequent, there have been some notable records of establishment, as shown in Table I.

Perhaps most notable is the existence of a small, relatively stable population in north-central Idaho, about 800 miles (1290 km) north of the northernmost native populations. These birds are "restricted to a narrow valley along the main Salmon

River and a tributary stream and valley called the Lemhi" (Blake *in litt.* 1956).

Marginal populations have been established along the southern edge of the Great Basin in Nevada, at locations such as Adaven, in the Grant Range, Nye County, and in the Pioche and Ursine areas, Lincoln County. These populations are insecure to the extent that periodic heavy snows virtually exterminate them, and they must be replenished by new stock from farther south.

Indicative of the many failures that have marked efforts to transplant these desert quail to other areas, McLean (1930) cites releases in Massachusetts, Pennsylvania, Kentucky, Oklahoma and Washington as unsuccessful, and Ridgway and Friedmann (1946) add Hawaii and Missouri to this list. In addition, releases in Wyoming (Anon. 1955) and Montana (Bent 1932) resulted in eventual disappearance of the released birds.

Even in states where the species is native, many attempts to extend its range have failed. McLean (1930) records failures in northern Arizona, northern New Mexico and eastern Colorado, and unsuccessful transplants to northern California localities are recorded by Grinnell *et al.* (1918) and McLean (1930).

Several such failures are known in Nevada. One was the transplant of 200 quail from Clark County to the Fallon area in Churchill County, in 1931. Another failure was the movement of about 100 birds from Overton, Clark County, to Steamboat Springs, south of Reno, Washoe County, in 1936. In 1950, the transplant of 40 Gambel's Quail from Bullfrog, in southern Nye County, to Twin Springs (at the south end of the Pancake Range) and Big Creek (Grant Range), farther north and east in Nye County, resulted in complete failure.

Local Distribution

Within the broad geographic range of this species there are many gaps in the local distribution of Gambel's Quail. Although Fig. 1 shows solid blocks of distribution in New Mexico, Arizona, California and northern Mexico, these birds generally occupy stringers of favorable habitat along drainage systems and the more or less isolated islands of suitable habitat on upland areas and the slopes of desert mountain ranges. The distribution is apparently more nearly continuous toward the center of this species' range than it is in the peripheral areas such as California, Nevada, New Mexico, Utah and Colorado.

In Nevada desert quail populations exist as discontinuous and often effectively isolated units (*cf.* Gullion and Christensen 1957). The valley populations in Nevada are restricted to the desert valley floors, where suitable vegetation is maintained by subsurface waters drained from surrounding or distant mountains. In Clark County the valley populations do not occur much above 2000 feet elevation (610 m above msl) and range down to the lowest corner of the state, 490 feet (149 m) in the Mohave Valley at the extreme southern tip of Nevada. In Nye County, valley populations are restricted to three areas (the Oasis Valley, Ash Meadows and Pahrump Valley), ranging from 2600 to 3400 feet elevation (790-1036 m). Major Lincoln County valley populations range the 30 mile (48 km) length of the Pahranagat Valley, from 2900 to 4000 feet elevation (880-1220 m), and are scattered as more or less isolated populations along the 80 mile (130 km) length of Meadow Valley Wash, from Rox, at about 2100 feet elevation (640 m), to Panaca (Meadow Valley), at about 4500 feet elevation (1370 m) (see Gullion *et al.* 1959 for a map showing these localities).

With the exception of the 3 isolated Nye County valley populations and 2 isolated Lincoln County populations (Coyote Wells and Pahranagat Valley), all of the valley populations are, or recently have been contiguous units. Prior to the construction of Hoover and Davis Dams and the filling of Lakes Mead and Mohave (in 1936 and 1951 respectively), these quail ranged the length of the Colorado River bottomlands in Nevada and tied together the Mohave, Las Vegas, Moapa and Virgin Valley populations. Now these groups are isolated from one another. The Virgin Valley population extends into adjacent parts of Arizona and Utah, and the quail in the Moapa Valley are in contact with those in the Muddy Valley, and more or less in contact with the scattered populations in the Meadow Valley Wash, in Lincoln County.

The distribution of the upland populations of Gambel's Quail is restricted to intermediate elevations on Nevada's desert ranges, usually at elevations of 3000 to 4500 feet (910-1370 m). These hill populations are best developed in the Dead Mountains, the Searchlight area and the Gold Butte-Bonelli Peak area in Clark County, and in the Mormon Mountains in southern Lincoln County. Other small, scattered hill populations occur in the other mountain ranges of Clark County and in a few of the southernmost ranges in Esmeralda, Lincoln and Nye Counties.

THE PHYSICAL ENVIRONMENT OF GAMBEL'S QUAIL

Altitude

Gambel's Quail have been recorded from at least as low as —200 feet (—61 m) elevation near Mecca, California (Grinnell and Miller 1944) to as high as 11,000 feet (3350 m), near the summit of Charleston Peak in southern Nevada (van Rossem 1936). However, the local plant environment and climate rather than altitude governs the permanent occupancy of a given habitat.

Maximum altitudes of normal occurrence of *L. g. gambelii* are given as 5400 feet (1640 m) in the Providence Mountains, California (Grinnell and Miller 1944), 4500 to 5000 feet (1370-1520 m) in Arizona (Griner *et al.* 1942), about 4000 feet (1220 m) in Utah (Greenhalgh *in litt.* 1955), and about 4500 feet (1370 m) in Nevada. Small scattered populations occur at higher elevations where they are generally restricted to small areas of exceptionally favorable habitat.

Extralimital populations of *gambelli* occur at 3900 to 4100 feet (1190-1250 m) elevation in Idaho (Blake *in litt.*) and at from 4000 to 7000 feet (1220-2130 m) in Utah (Greenhalgh *in litt.* 1956).

Colorado populations of *sanus* occur at altitudes of 4500 to 6000 feet (1370-1830 m) (Sandfort *in litt.* 1956) and this race occurs at from about 4900 to as high as 6500 feet (1490-1980 m) elevation in New Mexico (Ligon 1927). In the Rio Grande Valley, *ignoscens* ranges from about 2600 to 3900 feet (790-1190 m) elevation (Moore *in litt.*).

Soils

Perhaps it is not coincidence that the best Gambel's Quail populations on southern Nevada's desert uplands occur on residual soils of decomposed granite. The good populations in the Dead Mountains, the Searchlight area, and the Gold Butte area can be pointed to as examples. There are other ranges as high or higher in elevation as these, but composed of limestone, sandstone or igneous rocks, where quail densities do not nearly approach the densities of these 3 areas. The Charleston Mountains, (or Spring Mountain Range), McCullough Range and Muddy Mountains can be cited as examples of this latter situation. As compared to other soils, the granitic soils characteristically support a more luxuriant and diversified vegetation of the types suitable for quail occupancy, except, of course, for the transported soils of the valley bottoms, where sub-surface water permits a luxuriant growth of shrubs.

Campbell (*in litt.* 1957) notes that soil type possibly limits Gambel's Quail distribution in New Mexico just as it appears to in Nevada. He comments that preferred habitat types for this species "also occur in some parts of the state outside the range of Gambel's quail, for example, in the southeast. The soils of the southeastern part of the state (where there is certainly plenty of desert grassland, creosotebush desert, etc.) are mainly derived from limestone. Those of the southwestern and southcentral parts of the state, within the range of Gambel's quail, are mainly granitic."

Climate[2]

Table II summarizes the climatic factors affecting Gambel's Quail at selected Nevada localities, and Table III summarizes these factors for typical localities within the species' range throughout the southwest.

In Table II, Overton, Las Vegas, Pahrump and Beatty represent typical desert valley environments while Alamo and Caliente represent the climatic conditions at the edge of this species' intrusion into the Great Basin. Searchlight represents a typical upland or hill environment, while Pioche and Adaven represent the conditions endured by struggling Gambel's Quail populations at uppermost limits of their range. Boulder City is situated in unsuitable habitat midway between valley populations below and hill populations above.

Although Table II suggests that hill quail have the less severe summer environment, they actually encounter more severe temperature conditions than the quail in the valley habitats. Shade is much less dense and frequent, and soil surface temperatures in excess of 140°F (60°C) have been recorded where birds were actively foraging in the summer. The hill environment normally has low humidity, whereas the valley environment becomes 'sticky' with the humidity of transpiration from *Prosopis, Tamarix* and various other phraeophytes during the heat of summer.

Temperature

Examination of Table II indicates that Gambel's Quail survive best in Nevada areas where

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[2] In relation to climatic data, it must be stressed that for the purposes of this paper it has been necessary to rely upon the climatological data published by the United States Weather Bureau (U.S.D.A. 1941, and Weather Bureau 1950 to 1954). Although the best possible choice of stations has been made, these data may not always be representative of the microclimate in which the quail exist.

Table II. Climatic summaries for selected Nevada localities within Gambel's Quail range (from Weather Bureau, 1950-1954)

Locality	Elevation feet	Temperatures (°F)				Growing Season* days	Precipitation (inches)		
		Ave range	Mean ann.	Jan. mean	Jul. mean		Extreme annual	Mean ann.	Mean winter
a. Valley Situations									
Overton	1275	13.6-115.2	66.7	44.3	91.3	236	0.71- 5.89	3.58	2.30
Las Vegas	1878	17.8-113.2	66.1	44.5	89.7	241	0.56- 5.55	3.14	1.33
Pahrump[1]	2640	9 -109	64.1	42.1	85.2	214	— —	1.88	1.21
Beatty	3314	13.8-108.4	60.7	40.7	88.3	212	0.79- 8.36	4.14	2.87
Alamo[2]	3446	6.6-108.0	56.6	36.9	78.6	145	1.98- 6.88	5.01	3.05
Caliente[2]	4402	−0.4-104.6	53.8	32.4	77.0	151	2.92-11.52	7.71	4.25
b. Hill Situations									
Searchlight	3620	20.0-105.8	63.7	44.4	84.3	242	1.83-11.79	7.33	3.32
Boulder City[2]	2525	20.2-110.4	66.9	46.3	88.3	290	1.98- 8.87	4.90	2.18
Pioche[3]	6110	1.0- 98.8	51.6	31.3	74.3	154	7.14-16.32	11.60	6.45
Adaven[3]	6250	−1.4- 96.0	49.4	29.8	71.2	126	6.83-16.09	11.19	7.19

* Growing season—days between temperatures of 32°F or lower.

[1] Records incomplete, most data based on one year—1950.

[2] Marginal localities for Gambel's Quail.

[3] Extralimital populations.

Table III. Summarized climatological data for localities in Gambel's Quail range (compiled from U.S.D.A., 1941, and/or Weather Bureau, 1950-54)

Race	Population Status	Number of Stations	Temperatures (°F)			Growing Season* (days)	Precipitation (inches)	
			Extremes	Jan. mean	July mean		Annual mean	Winter mean
L. g. gambelii	Secure (range)	32	–16, +134	36.9-54.2	76.3-102.0	145-312	1.49-19.71	0.82-10.35
	(means)		7.1, +113.5	45.3	85.1	231	8.93	4.10
	Marginal (range)	7	–25, +117	31.6-47.4	72.8- 88.3	151-290	4.90-17.97	2.18- 9.64
	(means)		0.1, +110.6	41.0	81.4	213	10.16	4.31
	Extralimital (range)	11	–42, +112	17.8-32.8	64.6- 82.7	74-193	5.34-13.18	2.13- 7.40
	(means)		–22.4, +105.4	27.2	74.7	143	8.33	4.31
L. g. sanus	All populations (range)	7	–34, +105	23.0-31.9	70.5- 77.9	124-191	6.98-11.65	2.68- 5.50
	(means)		–22, +103	26.7	73.3	151	9.76	4.37
L. g. ignoscens	All populations (range)	5	– 5, +111	41.3-48.6	78.7- 84.2	206-238	5.25- 8.56	1.62- 2.83
	(means)		3.6, +108.4	45.2	81.4	219	7.00	2.26

* Growing season—days between temperatures of 32°F (0°C) or lower.

January mean temperatures do not drop below 40°F (4°C), and where subzero temperatures are unknown, although some good populations do exist in areas where January means are as low as 32°F (0°C).

The lowest January mean temperatures in the range of secure, native populations of *L. g. gambelii* in Arizona is 44°F (6.7°C), 41°F (5.0°C) in California, 37°F (2.8°C) in New Mexico, and 38°F (3.3°C) in Utah. Marginal populations exist where the January mean temperature drops as low as 31°F (−0.6°C) in New Mexico and 42°F (5.6°C) in Arizona. Extralimital populations of this race are established where January mean temperatures are as low as 17°F (−8.3°C) at Salmon, Idaho, 24°F (−4.4°C) at Loa, Utah, and 29°F (−1.7°C) at Adaven, Nevada. Except for stations in New Mexico and Utah, this race does not naturally occur where subzero temperatures are known. A −16°F (−27°C) at Socorro, New Mexico, seems to be the lowest temperature endured by *gambelii* in its natural range. However, extralimital populations have survived lows of —42°F (—41°C) at Greenriver, Utah, and —37°F (—38°C) at Salmon, Idaho.

On the other hand, the form *L. g. sanus* lives in Colorado habitats where January mean temperatures range from 23 to 30°F (—5- —1.1°C), and in New Mexico habitats where the range is 26 to 32°F (—3.3-0°C). Every locality occupied by this race experiences subzero temperatures, ranging from —34°F (—37°C) at Rifle, Colorado, to —8°F (—22°C) at Farmington, New Mexico.

The race *L. g. ignoscens* lives along the Rio Grande in Texas, where January mean temperatures range from 41 to 49°F (5.0-9.4°C). Surprisingly, this race experiences subzero temperatures, to —5°F (—21°C) at El Paso.

Apparently, it does not get too hot for Gambel's Quail in the southwest, since these birds survive at the Greenland Ranch in Death Valley, California, where maximum temperatures reach 134°F (57°C), the July mean temperature is 102°F (39°C), and the January mean temperature is a warm 51.6°F (11°C).

Growing Season

Nevada's largest and most stable Gambel's Quail populations are in localities where the average growing season exceeds 200 days a year. Prosperous but less stable marginal populations survive at Alamo and Caliente, where the growing season averages about 145 to 150 days, and an extralimital population exists under the conditions imposed by the 126 day average growing season at Adaven (Table II).

Elsewhere secure populations of *L. g. gambellii* exist in areas with growing seasons of from about 170 to as high as 312 days (Table III). In California the range is from 185 to 312 days; in Arizona from 189 to 274 days, in New Mexico from 169 to 214 days, and 2 stations in southwestern Utah both have 196 day growing seasons.

Marginal populations of this race live in areas with growing seasons varying from 166 to 238 days in Arizona and 183 to 231 days in New Mexico. Extralimital populations exist in areas with growing seasons varying from 123 to 193 days in Utah (the 74 day growing season at Loa being the exception), and the very short 109 days at Salmon, Idaho.

The race *L. g. sanus* lives in areas having a range from 124 to 191 days of growing season in Colorado, and 155 to 157 in the San Juan Valley of New Mexico.

L. g. ignoscens lives in an area with a growing season ranging from 206 to 238 days, well within the range of *gambelii* habitats.

Precipitation

Moisture-wise, a mean annual rainfall of 4.90 inches (124 mm) at Boulder City is insufficient to produce the vegetation necessary to sustain Gambel's Quail on Nevada's deserts (the low mean rainfalls for valley locations are not considered since plant growth there is supported by drainage from areas as much as 300 miles (480 km) distant in Nevada). However, the mean of 7.33 inches (186 mm) of rainfall at Searchlight provides the proper vegetation to support quail populations (Table II). Actually, means may be misleading. The amount of annual rainfall necessary to support this desert quail in Nevada may be somewhat higher than the recorded mean since there are many years of insufficient rainfall included in these means, years during which quail populations show a steady decline. Also, a substantial amount of the annual rain may fall in such a manner as to be of little or no value (*i.e.*; torrential mid-summer thundershowers, during which upwards of 3 inches of rain may fall in 2 or 3 hours and run off the baked soil so rapidly that moisture penetrates only the top 2 or 3 inches of soil).

It took 11.79 inches (298 mm) of rainfall at Searchlight in 1952 and 10.32 inches (262 mm) in 1954 to produce increasing quail populations in those years. The 9.61 inches (246 mm) recorded in 1951 did not suffice (although the 2.41 inches (61.2 mm) falling in the last 3 months of this year provided a good start for the 1952 season), nor did the 1.83 inches (46.4 mm) in 1950, or the 3.09 inches (78.4 mm) in 1953 even sustain existing populations.

Griner *et al.* (1942) note in Arizona that "heavy bird densities occur through many rainfall belts, although generally speaking the population index is light below an annual mean of 10 inches [254 mm]."

As pointed out elsewhere (Gullion 1954) the months of October to March have been found to be the critical months for adequate precipitation on Nevada deserts. Green feed is produced in quantity if rainfall is ample in October and if sufficient rain falls through the 5 succeeding months to sustain the growth of the plants that germinated in the moist, warm soil of early fall. This green feed apparently provides the vitamins and other nutrients necessary for the successful breeding activity of quail (*cf.* Lehmann 1953). Green food also provides succulence in the spring,

TABLE IV. Rainfall at Searchlight, Nevada—3620 feet elevation (from Weather Bureau monthly climatological data, 1949-1956)

Winter season	(RAINFALL IN INCHES)						Total	Quail Production yng/100 adults
	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.		
1949-50........	0 05	0.32	0.55	0.14	0.05	0.80	1.91	16
1950-51........	T	0.06	0.04	0.78	T	0.08	0.96	179
1951-52........	0.52	0.57	1.32	1.59	0	3.09	7.09	588
1952-53........	0	0.67	0.88	0.02	0.28	0.09	1.94	145
1953-54........	0.10	T	0.09	1.55	0 25	2.81	4.80	632
1954-55........	0	0.40	0.45	2.35	0.17	0	3.37	406
1955-56........	0	0.12	0.15	0.39	T	0	0.66	0

permitting widespread dispersal for nesting, independent of drinking water.

Table IV illustrates the influence of October to March rainfall upon Gambel's Quail production in one southern Nevada locality (see also Figure 2). Swank and Gallizioli (1954) consider December to April the critical months for winter precipitation in Arizona, otherwise the findings reported here generally agree with theirs.

From the data in Table IV, and those of Swank and Gallizioli (1954), it appears that a winter rainfall in excess of 5 inches (127 mm) is necessary to sustain high density Gambel's Quail populations on upland desert sites. Also, this rainfall needs to be fairly well distributed through the winter season to be of most value (*cf.* Gullion 1956*a*). Sufficient winter rainfall is not a reliable factor in the environment of the desert quail in California, Nevada or western Arizona, and accordingly quail populations fluctuate, often drastically.

Important in understanding the ecology of this quail on the southwestern desert areas is the fact that annual average precipitation increases from the west to the east across the southwest. and also that the percentage of rain falling during the summer months becomes progressively larger as more easterly localities are reached (see Figure 3). At the western edge of this species' range in California annual precipitation averages only about 4 inches (100 m) on the upland sites, and more than 70% of this falls during the winter. In southern Nevada the annual precipitation averages about one inch (25 mm) more, and only 60 to 70% of this falls during the winter. Farther east, in southeastern Arizona, the annual precipitation varies from 15 to 20 inches (380-500 mm), of which 60 to 70% falls during the summer months. The annual mean precipitation falls off sharply as the continental divide is crossed to the eastward, dropping to about 8 inches (200 mm). Still the pattern of heavy summer precipitation persists, with 60 to 80% of the annual mean coming in that period.

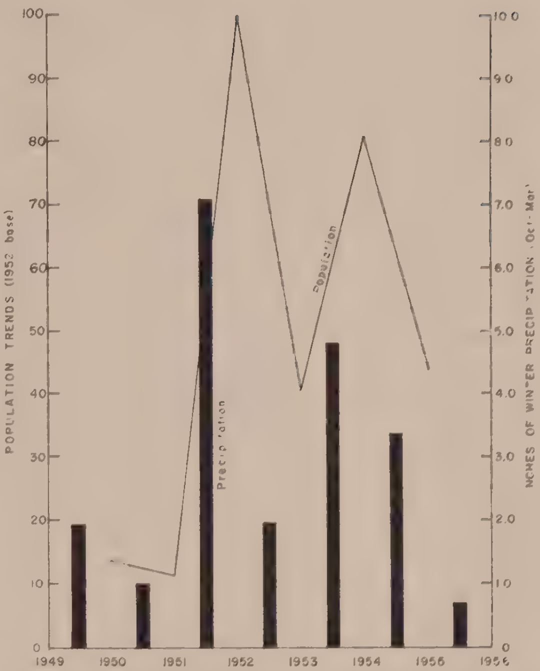

FIG. 2. The fluctuations of Gambel's Quail populations as related to October-March precipitation at Searchlight, Nevada, 1949-1955.

Snowfall

Summarized snowfall data are not readily available and therefore it is difficult to analyse in detail the relationship of Gambel's Quail distribution to snowfall. However, it appears that, like other members of the genus *Lophortyx* and the closely related *Oreortyx,* the desert quail have little tolerance for snow and few secure desert quail populations exist in areas where total annual snowfall exceeds 20 inches (500 mm), or where one or more inches (25+ mm) of snow is on the ground for more than about 40 days a year (U.S.D.A 1941).

The better populations of this species occur where the mean annual snowfall is less than 5 inches (127 mm), and snow cover exists for less than 20 days a year.

In considering the occurrence of Gambel's Quail in relation to snowfall at the higher and/or colder localities, such as those in Idaho, Utah, Colorado and New Mexico, it is important to note that all of these sites have relatively low percentages of their total precipitation in the winter period. Although the mountains surrounding these valleys may receive very heavy winter snows, the snow-

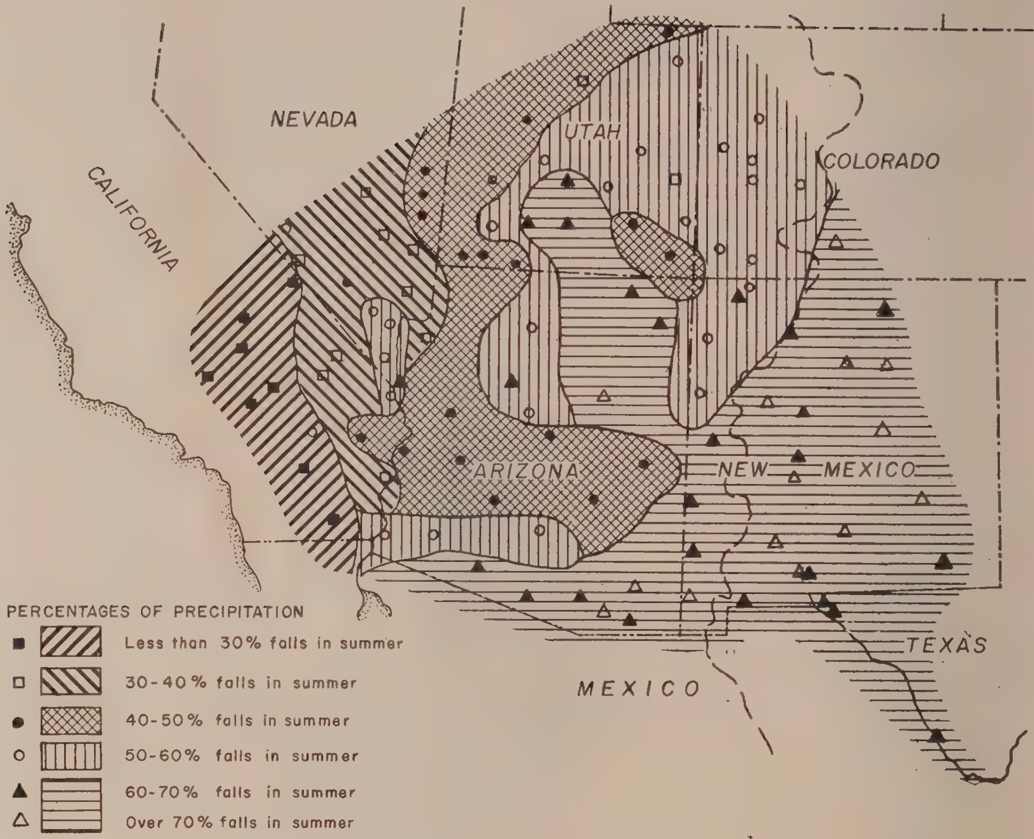
NEVADA
CALIFORNIA
UTAH
COLORADO
ARIZONA
NEW MEXICO
TEXAS
MEXICO
PERCENTAGES OF PRECIPITATION
■ ▨ Less than 30% falls in summer
□ ▧ 30-40% falls in summer
● ▩ 40-50% falls in summer
○ ▥ 50-60% falls in summer
▲ ▤ 60-70% falls in summer
△ ▤ Over 70% falls in summer

Fig. 3. The pattern of summer precipitation on the American southwestern desert regions.

fall in the valleys occupied by quail is notably light, and typically does not persist as a complete ground cover for any long period of time. At Salmon, Idaho, 40% of the annual precipitation is in winter; at the higher locations in Utah about 40% occurs in winter; at all Colorado sites only about 45% of the precipitation falls in the winter; and at the two San Juan Valley locations in New Mexico only 38 to 45% of the precipitation comes during the winter months.

Evaporation

The effectiveness of precipitation in producing the vegetation that constitutes habitable range for Gambel's Quail is limited by the rate of evaporation, particularly in relation to amounts and seasons of precipitation. In southern Nevada and southeastern California, where the least precipitation occurs during the summer, the importance of this factor is particularly pronounced.

The seriousness of this relationship in affecting quail populations was forcefully demonstrated during the spring and summer of 1953. The 4.23 inches (107 mm) of precipitation which had fallen at Searchlight from September to December, 1952, had produced a carpet of green annuals on the desert. When annual plant plots were being read during the latter part of February, 1953, *Lotus tomentellus* and *Erodium cicutarium* were commencing an early flowering period, and there was every indication that quail productivity for the 1953 season would even exceed the phenomenal production of 1952 (*cf.* Gullion 1956*b*). However, the last significant rainfall on the desert was about December 20, 1952, and strong, drying winds commenced during the latter part of February, and continued unabated for the next 3 months. Soil moisture was rapidly dissipated, and the annuals depending upon that moisture soon became desiccated. A recheck of the plant plots in May, 1953, revealed that many of the plants were still intact, with nearly normal flower and leaf color, but dry as herbarium specimens, and brittle to the touch.

The effect of this upon quail production was disastrous (Table V). Although the simulus provided by winter greens was sufficient to induce

TABLE V. Status of Gambel's Quail reproduction in southern Nevada—June-July

Site	Nunber of Potential ♂♀s				Percentage of ♂♀s With Broods				Average Brood Size[1]				Percentage of Potential Production Realized[2]			
	1951	1952	1953	1954	1951	1952	1953	1954	1951	1952	1953	1954	1951	1952	1953	1954
Guzzler S-4	19	25	40	30	53	48*	75	97	6.2	11.7	4.0	8.1	33	113+	30	105
Guzzler GB-4	—	15	50	47	—	53*	46	85*	—	9.5	4.6	11.2	—	104+	21	96+
Guzzler GB-11	—	10	55	68	—	90	47	77*	—	11.6	4.5	8.3	—	104	21	66+
Guzzler D-1	—	23	—	60	—	35*	—	88*	—	11.5	—	10.7	—	153+	—	102+
Guzzler D-16	—	6	59	42	—	67*	68	86*	—	8.8	3.8	9.6	—	218+	26	84+
Totals	19	79	204	247	53	52*	58	85*	6.2	10.9	4.2	10.0	33	130+	24	88+

[1] Includes all age classes.

[2] Using the figure 10.0 as average brood size—this being approximately the average achieved in the 2 highly productive years 1952 and 1954 (actual area-wide figures—10.6 in 1952, 9.96 in 1954).

* Presence of 'weaned' chicks in the population indicates a higher percentage than given here—*i.e.*, double-brooding, with at least some of the pairs recorded as being unproductive actually having produced one brood earlier and at the time of this count being in the process of laying or incubating a 2nd clutch (see Gullion 1956*b*). This was of more consequence in 1952 than in 1954, hence the difference in the relative figures. Percentage of ♂♀s producing broods probably exceeded 90% at all sites in 1952.

+ Includes the total of 'weaned' chicks not in broods.

early breeding activity (in late February) and successful nesting, the loss of green food brought the nesting season to an early cessation. Apparently the loss of the insect crop reduced the survival of the chicks which did hatch, since average brood size was only 4.2 chicks per brood, as compared with 10.0 or more chicks per brood during the preceding and succeeding year (see Table V). Not only was the average brood small, but renesting was insignificant, and more than 40% of the potential breeding pairs failed to produce surviving broods (as of the end of June). Small brood size and low percentage of successfully producing pairs resulted in a net production of only 24% of the potential productivity. In addition, in 1953, not only was initial chick production low, averaging about 140 young per 100 adults in late June, but survival was poor, with the young-adult ratio dropping to less than 90 chicks per 100 adults by early August, and about 20 young per 100 adults in November.

It is probably significant that the distribution of this species of quail (secure, marginal and extralimital populations) coincides with the area of the highest rate of evaporation on the continent (the "over 240 cc" zone of Livingstone and Shreve 1921).

The range of Gambel's Quail not only coincides with the area of very high evaporation, but it is also an area of extremely low precipitation and high summer temperatures—all factors which increase the severity of each of the other factors. Table VI gives some precipitation-evaporation data for a few selected stations within this species' range in the southwest.

TABLE VI. Evaporation rates in Gambel's Quail range

Station	Mean Annual Precipitation (inches)	Mean Annual Evaporation* (inches)	Ratio of Evaporation to Precipitation
Backus Ranch, Calif.	4.67	113.54	24.31
Boulder City, Nevada	4.90	111.62	22.78
Davis Dam, Arizona	5.17	114.69	22.18
Yuma, Arizona	1.72	101.72	59.14
Sacaton, Arizona	8.53	102.49	12.02
Bosque del Apache, N.M.	6.60	102.16	15.48
Agricultural College, N.M.	5.25	98.64	18.79
Montrose, Colorado	9.52	63.35	6.65

* Evaporation is measured in the standard Weather Bureau type pan of 4 foot diameter.

Distribution of Water

The importance of drinking water as a factor limiting the distribution of Gambel's Quail on the desert has been much debated. Grinnell *et al.* (1918), Grinnell (1927), and McLean (1930) maintained that the need for daily watering is an important factor restricting the distribution of this species. Vorhies (1928) and Gorsuch (1934), on the other hand, believed that daily watering is not a factor limiting the distribution of this species. McLean (1930) credited a Mr. Ragsdale with stating that these birds could survive on the desert on the succulence of green plants alone, and Griner *et al.* (1942) supported this observation, also noting that insects furnished additional moisture.

Observations made in southern Nevada during the present study show that watering needs of Gambel's Quail cannot be described as a simple "they need drinking water" or "they do not." In the desert valley areas where the Desert Riparian and Thorn Shrub types occur, or where there are irrigated crops, or streams or waste waters are present, a combination of high humidity and fleshy plants provides the moisture needed for the survival of this species, even during the hottest part of the year. In this situation desert quail, if necessary, can live their life-span without taking a drink of water.

On the desert uplands the situation is more complex. During the greater part of the year temperatures remain moderate, and even though humidity may remain low, the moisture needs of the quail can be met by the water taken in as plant succulence or in the bodies of insects. There is some indication that at least some metabolic water may be conserved, especially in areas where the seeds of certain legumes (*Lotus* and *Astragalus*) are important sources of food. During rainy periods water is readily available, and, although rains may not be dependable during winter periods, thunderstorms usually provide a widespread source of moisture on the Nevada deserts during late summer. Perhaps the most important aspect of these summer storms is the myriad of succulent seedlings of desert ephemerals (especially *Erodium*), which may appear within 48 hours after a storm has passed.

On Nevada desert areas the critical period during which water may be an important factor limiting quail distribution extends from about the middle of June to mid-July. This is the period when average daily maximum temperatures reach or exceed 100°F (38°C), after most of the succulent spring annuals have withered, and prior to the onset of the summer thunderstorm activity. Normally, for 11 months of the year the distribution of water is probably unimportant as a factor limiting quail distribution in southern Nevada. However, during that 12th month the proper distribution of water can be extremely important.

It is during this period that the desert upland habitats which furnish adequate food supplies must have a proper distribution of water if Gambel's Quail are to make maximum use of this environment in Nevada. It is for this brief period of time that the development of artificial watering structures in areas of otherwise suitable habitat becomes a practical and useful game management technique (see also Gullion 1956*a*).

THE VEGETATIVE ENVIRONMENT OF GAMBEL'S QUAIL

In the final analysis the natural vegetation of a site represents the sum of the interactions of the various elements of the physical environment. With this in mind the vegetative environments in which Gambel's Quail survive, either as natural or extralimital populations, have been investigated and are described for Nevada and the other western states.

Nevada

I have noted earlier that the distribution of Gambel's Quail in Nevada consists of disconnected and often effectively isolated populations. To understand this pattern of distribution a close examination has been made of the vegetation types these quail occupy, and an attempt made to determine how these types provide this bird with its year-long needs. The study sought the factors which make one area suitable quail range, and often amendable to management, while another area remains uninhabited, even when drinking water is readily and permanently available.

Valley Habitats

The vegetation comprising the habitat of Nevada's valley populations of Gambel's Quail is often luxuriant when compared to the surrounding desert. A considerable portion of this land in southern Nevada is under cultivation, with crops such as cotton, alfalfa and truck-gardening predominating. These fields often are small, surrounded by fence-lines grown up to *Atriplex lentiformis, Lycium Torreyi, Prosopis juliflora* or *P. pubescens,* and/or annual weeds.[3]

Where the land is not under cultivation the valley areas are often covered by dense, brushy areas of Thorn Shrub, Saltbush and Desert Riparian habitat types. These types normally provide all the needs of this quail in abundance. The often dense tangles of *Pluchea sericea, Prosopis juliflora* and *P. pubescens, Tamarix pentandra, Phragmites communis, Baccharis glutinosa* and *Atriplex* spp., characteristic of these types, provide excellent cover for quail. In addition, the *Prosopis* (and *Phoradendron californicum* parasitic on *Prosopis*), *Atriplex lentiformis, Lycium Torreyi,* and a number of noxious weeds such as *Amaranthus retroflexus, Chenopodium* spp., *Bassia hyssopifolia, Helianthus annuus, Melilotus albus, Sorghum halepense, Echinochloa crusgalli* and *Sphaeralcea* sp., as well as various cultivated plants, furnish an abundant supply of food, both seeds and greenery.

In the more northerly valleys, such as the Pahranagat and Meadow Valleys in Lincoln County, the vegetation becomes more characteristic of a Great Basin environment. In the Pahranagat Valley some of the shrubs from the lower, warmer desert valleys persist, but the major shrub cover consists of a Basin Riparian type, including *Sarcobatus vermiculatus, Chrysothamnus nauseosus, Salix* spp. and *Populus Fremontii.*

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[3] Botanical nomenclature follows Kearney and Peebles 1951, wherever possible.

Still farther north, and at a higher elevation, a marginal Gambel's Quail population exists in the Meadow Valley amid a Greasewood type, consisting of extensive areas of *Sarcobatus vermiculatus,* interspersed with *Chrysothamnus nauseosus,* and scattered *Artemisia tridentata.* In both of these valleys most of the noxious weeds listed above furnish seeds for food. In addition *Salsola Kali, Amaranthus graecizans, Wislenzia refracta* and *Cleome serrulata,* as well as alfalfa and small grains, add to the food resources of these areas.

Drinking water is often available in the desert valley situations, either as streams, irrigation water, or waste water. Where water is not available in the free state, moisture can be readily obtained from the succulent leaves and stems of plants such as *Lycium Torreyi, Suaeda fruiticosa, Heliotropium curassavicum, Sarcobatus vermiculatus,* and several other fleshy species. Moreover, the humidity is normally high in the valley habitats, so basic moisture needs are much less than in drier, upland sites.

It is hardly surprising that the valley situations support the most dense quail populations, or that there is normally less year-to-year fluctuation in quail abundance in these valley populations than in hill populations (Figure 4).

However, in the absence of free water the Thorn Shrub type has a low carrying capacity for quail when it consists of pure stands, or bosques, of *Prosopis juliflora.* Mesquite alone does not provide a livelihood for the desert quail and substantial numbers will be found only where the heterogeneous association noted above occurs. Similarly, in the absence of free water the Saltbrush type is a poor quail habitat unless some of the succulent-leaved plants are present.

Hill Habitats

The vegetation of the hill habitat differs markedly from that of the valley areas. There are at least 5 distinct habitat types available within the range of physical conditions tolerated by Gambel's Quail. These types are Bur-sage, Blackbrush, Desert Grassland, Desert Shrub and Browse Shrub. However, only one of these, the Desert Shrub type, offers the environment conducive to the development of substantial desert quail populations.

Basically the Desert Shrub type consists of a somewhat variable combination of microphyllous shrubs which usually includes *Acacia Greggii, Lycium Andersonii, Krameria parvifolia, Thamnosma montana, Acamptopappus sphaerocephalus, Dalea Fremontii, Hymenoclea salsola, Opuntia basilaris, O. acanthocarpa* and other *Opuntia, Echinocereus Engelmannii, Echinocactus acanthodes, Yucca schidigera* and other *Yucca, Salvia carnosa, Ephedra viridis, Larrea tridentata, Eriogonum fasciculatum, Viguiera deltoidea,* and a few other shrubs.

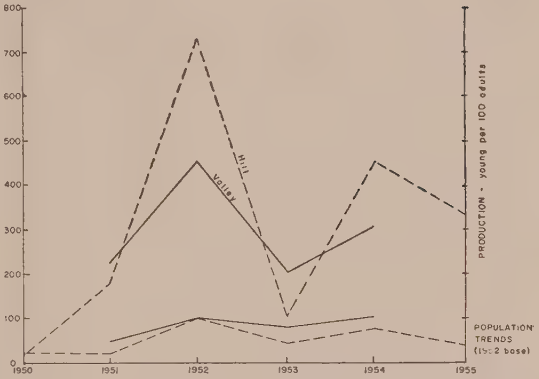

FIG. 4. A comparison of the annual production and fluctuations of hill and valley populations of Gambel's Quail in southern Nevada, 1950-1955.

Within this general Desert Shrub type several well defined sub-types can be recognized. Three of these 5 sub-types prove to be the most acceptable habitats for Gambel's Quail in the hill environments. These 3 are the Colorado Desert Shrub, High Desert Shrub and Desert Wash Shrub subtypes, although in some locations the Low Desert Shrub sub-type also proves to be an acceptable quail habitat. These sub-types have in common a considerable diversity of shrub species, usually including most of those listed for the type, but each is dominated by certain prominent shrubs which denote them as being distinct from the other sub-types.

Where the Colorado Desert Shrub enters Nevada (at 500 to 2000 feet (152-610 m) elevation) *Hyptis Emoryi, Dalea spinosa, Opuntia Bigelovii, Fouquieria splendens* and *Encelia farinosa,* in particular, join many of the species listed above to provide a highly diversified sub-type with ample food and cover for the desert quail. Next above the Colorado Desert Shrub is a Low Desert Shrub sub-type (at 2000 to 3500 feet (610-1060 m) elevation), a somewhat variable mixture of desert shrubs, but with *Franseria dumosa* invariably present, and *Mendora spinescens, Krameria parvifolia* and *Yucca schidigera* often present. Although this sub-type varies from a poor to a good quail habitat, it is most often lacking in desirable food species—especially where the vegetation is limited to *Franseria dumosa, Menodora spinescens, Krameria parvifolia, Larrea tridentata* and scattered *Opuntia basilaris.*

At higher elevations (3500 to 4000 feet—1060-1210 m) the High Desert Shrub sub-type occurs. *Coleogyne ramosissima* replaces *Franseria dumosa,* and *Lotus rigidus, Salazaria mexicana, Eriogonum fasciculatum* and *Yucca baccata* become prominent along with many of the other typical desert shrub species. This sub-type is certainly the most extensive high-density quail habitat on Nevada desert uplands, and it is the type most amendable to habitat management in the form of water development. Cover is always adequate in this type and, if food is sufficient anywhere on the desert ranges, it will be so in this environment. However, the best hill environment of all is provided by the Desert Wash Shrub sub-type, where *Acacia Greggii, Chilopsis linearis, Lycium pallidum, Cassia armata, Hymenoclea salsola, Salazaria mexicana* and *Prunus fasciculata* create extensive dense clumps of thorny or spiny escape cover. Although this sub-type is normally not more than a few hundred feet wide, it often extends for several miles into less favorable habitat and, by providing a localized area of optimum habitat, permits quail to persist in situations where survival would otherwise be unlikely.

Sources of moisture vary considerably in the Desert Shrub. In some areas springs, seeps or stock-watering developments provide drinking water for quail, and in a few areas abundant succulent-leaved plants such as *Lycium pallidum* and *L. Andersonii, Euphorbia albomarginata* and *E. serpyllifolia,* and other plants, provide sufficient moisture to sustain quail populations.

Several of the prominent perennial species comprising the Desert Shrub type produce important quantities of seeds which are taken by Gambel's Quail. *Acacia* (and the *Phoradendron* parasitic on *Acacia*), *Dalea, Chilopsis, Thamnosma, Euphorbia, Lycium, Sphaeralcea ambigua, Viguiera* and *Encelia,* in particular, fall into this category.

It is in the Desert Shrub type that the seeds of the ephemeral *Lotus* (especially *L. tomentellus* and *L. humistratus*), *Lupinus sparsiflorus, Astragalus Nuttallianus* and *Erodium cicutarium,* which seem to be the key to Gambel's Quail abundance or scarcity on Nevada desert uplands, are most abundantly produced. Also, a number of other ephemeral plants, which are less important but nevertheless contribute to the overall sustenance of the quail population, occur. Included in this group are *Cryptantha* spp., *Mentzelia nitens* and *M. tricuspis, Boerhaavia Wrightii* and *Cuscuta* spp.

Of particular interest is the close relationship between the occurrence of the shrub *Thamnosma montana* and the highest density Gambel's Quail populations on Nevada desert areas. Although the seeds of this pungent plant occur regularly in small numbers in the crops of desert quail, I do not believe that the occurrence of this shrub has a direct influence upon the distribution of these quail. Rather, I feel that the summation of climatic and edaphic factors which favor the growth of this shrub similarly encourage the growth and limit the distribution of the ephemeral and perennial plants which provide the preferred and most reliable food supplies for this quail. The relationship suggests that turpentine-broom, *Thamnosma montana,* may be a good indicator of the best desert upland habitats for Gambel's Quail in southern Nevada.

The Desert Shrub habitat may support fairly high densities of quail under the proper conditions (as many as 500 birds per square mile), but these populations are not so stable as those in the valley habitats (Fig. 4). However, this is the environment which shows the greatest potential for substantial increases in desert quail populations through habitat improvement.

Many of the most conspicuous ephemeral plants appearing on the desert during years of adequate moisture contribute little to the maintenance of the desert quail. Particularly showy and abundant during desert blooms are the evening-primroses (*Oenothera multijuga* and *Oe. caespitosa*), *Phacelia crenulata,* various crucifers (especially *Lesquerella Palmeri, Descurainia pinnata* and *Dithyrea californica*), composites (*Baileya pleniradiata, Chaenactis steveoides, C. Fremontii* and *Malacothrix californica*), buckwheats (*Eriogonum Wrightii, E. nidularium* and others), Indian-wheat (*Plantago insularis, P. scariosa* and others), and the golden poppies (*Eschscholtzia minutiflora* and *E. glyptosperma*). In spite of the tremendous abundance of seeds produced, these species do not appear as quail food until preferred seeds are in short supply, and then the appearance of these seeds as quail foods is indicative of failing food supplies, and imminent declines in quail populations.

These showy annuals typically occur in the Bursage type (usually included in the Creosotebush type or zone by others—*cf.* Billings 1951). This type, dominated by *Franseria dumosa* and *Larrea tridentata,* is normally shunned by Gambel's Quail and is incapable of sustaining their populations for more than a few weeks during the most favorable period of a desert bloom.

It should be noted that 2 of the plant groups most conspicuous on the southwestern deserts, the cacti and the yuccas, appear to contribute virtually nothing to the sustenance of this quail. The yuccas (particularly the arborescent *Y. brevifolia*) provide some cover and, in Nevada, only the seeds of *Echinocactus acanthodes* (of 19 species of cacti common in the area) are utilized as food by Gambel's Quail, and then incidentally.

In addition to the 2 hill habitat types already mentioned (Desert Shrub and Bur-sage), the Desert Grassland, Blackbrush, and Browse Shrub types are all within the range of the climatic tolerances of the desert quail. The Desert Grassland type consists primarily of stands of *Hilaria rigida* and scattered *Larrea tridentata, Eurotia lanata, Franseria dumosa* and *Acamptopappus sphaerocephalus*. The Blackbrush type consists of *Coleogyne ramosissima,* with a sprinkling of other species such as *Eriogonum fasciculatum, Larrea tridentata,* and sometimes forests of *Yucca brevifolia.* The Browse Shrub type is a higher elevation association, usually present on the middle slopes (5000 to 7000 feet elevation—1600-2300 m) of the desert mountain ranges, and may include *Quercus turbinella, Garrya flavescens, Ceanothus Greggii, Rhus trilobata, Cowania mexicana,* and *Arctostaphylos pungens.* All 3 of these types are notably deficient in the production of the preferred ephemeral food plants. Only the Desert Grassland has any real abundance of ephemeral plants, these being more or less limited to the normally unutilized *Eriogonum-Chaenactis-Oxytheca* group. The Blackbrush and Browse Shrub types have relatively few ephemeral plants even during moist years. Quail occasionally wander into these vegetation types but their presence is normally of temporary nature, and a result of dispersal from centers of high populations, abnormal abundance of preferred foods in these normally marginal areas for a limited time, or a depletion of food supplies in preferred habitats.

California

Grinnell and Miller (1944) noted this species' habitat in California to be "Thickets and adjacent more or less open ground, usually within reach of water (permanent springs or streams) for daily use, at least during certain seasons of year. Tracts or clumps of mesquite [*Prosopis juliflora*], screwbean [*P. pubescens*], catclaw [*Acacia Greggii*] and a certain kind of saltbush (*Atriplex lentiformis*) each provides suitable safe cover and other favoring factors for this quail."

In 1951, in the Providence Mountains of eastern San Bernardino County, I saw Gambel's Quail in a well developed desert shrub vegetation, much like that described as the High Desert Shrub subtype in Nevada.

Arizona

Griner *et al.* (1942) evaluated the relationship of Gambel's Quail to the vegetation types in Arizona. They found the pure grassland, Creosotebush, Saltbush, Browse-shrub (Chaparral) and Pinyon-Juniper types all to be poor or marginal environments for this quail. However, they note that these types may be invaded temporarily "to harvest the ephemeral greenery and subsequent seed crop that is produced by the weeds and annuals following the winter and summer rains."

They state that the Desert Shrub type "embraces the largest areas of any type in the Gambel quail range. Its total quail population is undoubtedly greater than for any other type, and it is believed to be second only to the mesquite in unit density." Griner *et al.* list *Canotia holacantha, Cercidium floridum* and *C. microphyllum, Holacantha Emoryi, Fouquieria splendens, Olneya Tesota, Franseria deltoidea* and *F. dumosa* as components of this type. Gallizioli (*in litt.* 1955), believing this type now to be Arizona's most important quail range, adds *Prosopis juliflora, Acacia Greggii, Mimosa* sp., *Celtis pallida* and *C. reticulata, Lycium pallidium, Condalia* sp., and several chollas and prickly pears (*Opuntia* spp.).

Griner *et al.*, in 1942, believed that the Mesquite or River Bottom type, although the smallest total area of quail habitat in Arizona, is "the type with the greatest production potential for quail, and today has the heaviest densities of any of the types." They list dependable water supply, excellent cover and a dependable food supply as the reasons for this type's high preference. However, in 1955, Gallizioli (*in litt.*) stated that many of the river bottom areas have been cleared for cultivation and now support few if any quail. He further believes that the extensive undisturbed mesquite bosques have quail densities far below those of Desert Shrub areas.

Griner *et al.* listed the cultivated lands along Arizona's river valleys as important quail habitat and as the one situation where food and cover might be manipulated to benefit this species.

According to a description of the habitat on the Santa Rita Experimental Range, Arizona, given to me by Reynolds (*in litt.*) and Gallizioli (*in litt.* 1955) it appears that the quail studied by Gorsuch (1934) lived in what would now be classed a Grassland-Mesquite type (see also Humphrey and Mehrhoff 1958).

Gallizioli (*in litt.* 1957), after having reviewed the preceding text of this section, pointed out:

> ". . . in Arizona perennial grasses are an important component of the ground cover of much of our best quail habitat. On our Oracle Junction study area quail density on one portion of our hunt area which has an abundance of perennial grasses of several species is markedly higher than on the adjacent, more heavily grazed areas where grass is more sparse. I believe the grasses are important largely from the standpoint of cover. In other areas, west of Prescott for example, where severe overuse has eliminated most of the perennial grasses from the desert shrub type, quail are most abundant in places where stands of the coarse tobosa grass (*Hilaria mutica*) are still found."

New Mexico

Campbell (*in litt.* 1956) lists 4 principal types of Gambel's Quail habitat in New Mexico. "These are (1) the mesquite thicket or river bottom type, (2) the desert grassland, (3) the creosotebush desert, and (4) river valleys in the sagebrush desert. The first 3 of these include most of the main range of the species in New Mexico, and occur in the southwestern and south central parts of the state."

The "mesquite thicket or river bottom type" consists of dense stands of *Prosopis* and *Tamarix,* and abundant cottonwoods (*Populus* sp.). "Unfortunately for quail, much of this . . . type has been cleared for agriculture (cotton, alfalfa, etc.)." (Campbell *in litt.* 1957).

Larrea tridentata and *Flourensia cernua* are very important components in the creosotebush desert, and are frequently present, but much less common, in the desert grassland. Other characteristic plants of both the grassland and creosotebush desert in New Mexico are *Prosopis juliflora, Rhus microphylla, Acacia constricta* and *A. Greggii, Mimosa biuncifera, Condalia* sp., *Lycium* sp., *Chilopsis linearis,* various *Opuntia* spp., *Yucca elata,* and *Quercus* sp. (shrub live-oak).

Campbell comments that Gambel's Quail do not permanently occupy pure stands of *Larrea* and *Flourensia,* but are found along brushy washes in well-developed creosotebush desert areas. The desert grassland type occupied consists of a mixture of grasses and shrubs with few if any quail in regions of pure desert grassland.

The 4th habitat type, "river valleys in the sagebrush desert," occurs in "the extreme northwestern part of the state, in the valley of the San Juan River and its tributaries" (Campbell *in litt.* 1957). The habitat occupied seems to be typical sagebrush type, with *Artemisia tridentata, Populus* sp., *Chrysothamnus* sp., *Rhus microphylla,* and *Clematis ligusticifolia.* Gambel's Quail exist in fairly large numbers in this region but are almost entirely confined to the valley bottoms.

Texas

Moore (*in litt.*) says of the environment of the Gambel's Quail in Texas:

> "The range of this quail is limited to the Upper Rio Grande Valley from El Paso to the vicinity of the Chisos Mountains. At no point does it range more than twenty miles [32 km] from the river, in fact, it is usually confined to the river bosque. This area consists of overflow country from the Rio Grande. Cultivated fields of alfalfa and cotton also are located nearby and inhabited by the Gambel. This species is more dependent on a constant supply of water than are other Texas quail. Since this bird occupies only the river areas the vegetational types preferred are limited."

Moore lists *Tamarix pentandra, Prosopis pubescens* and *P. juliflora, Lycium* sp., *Celtis pallida, Chilopsis linearis, Acacia Greggii* and *A. constricta,* and *Ungnadia speciosa* as growing along the Rio Grande where Gambel's Quail occurs. He adds, "Included within the quail's range of course are the various cacti and yuccas. Creosote bush and tarbush, *Flourensia cernua,* are also ever present."

Colorado

Sandfort and Gilbert (1954) describe the habitat of Gambel's Quail in Colorado as follows: "They are found commonly along the brushy arroyos, drain ditches, river and creek bottoms and brushy mesas throughout their range. Dense thickets of greasewood [*Sarcobatus* sp.], tamarisk [*Tamarix* sp.], and skunkbush [*Rhus* sp.] often make hunting of this bird extremely difficult . . . ." Sandfort (*in litt.* 1956) adds that these birds occur most frequently adjacent to agricultural lands, but also "Coveys occur along the river valleys . . . in areas remote from agriculture. Birds occasionally are found in the piñon-juniper type."

Utah

Greenhalgh (*in litt.* 1955) comments that the Gambel's Quail habitat in southwestern Utah is similar to adjacent areas in Nevada, consisting of *Coleogyne ramnosissima, Larrea tridentata, Prunus fasciculata, Opuntia* spp., *Yucca brevifolia* and other species of *Yucca.* Farther north and east *Artemisia, Sarcobatus, Atriplex, Chrysothamnus* and *Rhus* become this quail's habitat. In the more northern and eastern parts of Utah these birds are limited to the edges of farmland, where "There is usually some heavy brush as squaw brush [*Rhus* sp.] etc. present." Greenhalgh notes in some areas of central Utah that California Quail (*Lophortyx* *californica*) and Gambel's Quail occur together. The former species occupies the cultivated field areas and the latter stays in the drier sagebrush areas adjacent to the fields.

Idaho

Blake (*in litt.*) says that the extralimital population of Gambel's Quail in northcentral Idaho lives in an area where pastures, hay and grain fields are common. He reports that most of the coveys he has seen have been on the edge between the cultivated fields and stands of natural vegetation, the latter consisting of *Artemisia tridentata, Sarcobatus vermiculatus, Atriplex canescens* and *A. confertifolia, Chrysothamnus nauseosus,* and *Opuntia polyacantha.* Blake also indicates that a number of larger shrubs and trees occur in this area, some of which would provide good cover during brief periods of heavy snowfall. These include *Cornus sericea, Ribes aureum, Rhus trilobata, Toxicodentrum radicans, Symphoricarpos tetonensis,* and "a profusion of rose thickets and clematis."

Mexico

Leopold (1959) indicates that this quail occurs in the mesquite grasslands and deserts, frequenting "the mesquite and hackberry thickets along washes and on the flats." He further describes the vegetation of the preferred quail habitats on the Colorado River delta as being a "combination of mesquite and such weeds as wild hemp [*Sesbania* sp.], tornillo [*Prosopis pubescens*], and arrowweed [*Pluchea sericea*], . . ." In Sonora, Gambel's Quail are relatively abundant "where mesquite stands are interspersed with open patches of grama grass and seed-bearing annuals."

EXPERIMENTAL EVIDENCE OF HABITAT SUITABILITY

Earlier it was noted that many releases of transplanted Gambel's Quail in habitats quite different from their native desert haunts have resulted in failures. These failures in areas far removed from the southwestern desert are to be expected, and the rare successes are of more interest. However, the failure of wild-trapped Gambel's Quail to survive when transplanted into typically southwestern desert habitats within the limits of the climatic tolerances of the species is of considerable importance in the evaluation of habitat requirements.

Observations upon naturally developed and introduced Gambel's Quail populations at many of the artificial water developments described earlier has permitted such an evaluation. Since few quail, if any, existed in the areas where most of these guzzlers were installed during the 1948 to 1950 period, the record of quail population increases, and daily usage, provides a definite clue to the value of the various vegetation types as quail habitats.

TABLE VII. Guzzler usage compared on habitat types

Habitat Types[2]	DAILY BIRD UTILIZATION (numbers of birds)[1]					Total Units
	Heavy 150-800+	Moderate 75-150	Light 20-75	Incidental 1-20	None	
HS	22	1	0	0	0	23
HS-LS	4	0	0	0	0	4
LS	7	1	1	0	2(1*)	11
Cra	2	1	1	0	0	4
Cra-HS	1	0	0	1	0	2
Cra-DW	1	0	0	0	0	1
DW-DG	2	0	0	0	1*	3
DG-LS	0	1	0	0	0	1
LS-DW	0	0	1	0	0	1
CS	1	0	0	2	0	3
CS-Fdu	0	0	0	1	0	1
Fdu	0	0	0	0	4	4
Fdu-LS	0	1	0	1	4	6
Fdu-DW	0	0	1	0	0	1
Totals	40	5	4	5	11	65

[1] Utilization—average daily usage during late June-early July period of critical water needs in 1953 and 1954.

[2] Habitat Types—HS—High Desert Shrub; LS—Low Desert Shrub; CS—Colorado Desert Shrub; DW—Desert Wash Shrub; DG—Desert Grassland; Cra—Blackbrush; Fdu—Bur-sage.

* Persistent leaker, evaluation uncertain.

Table VII summarizes the distribution of the 65 guzzlers in southern Nevada in terms of quail usage and surrounding habitat type. It is apparent from this table that most of the guzzlers heavily used by quail in 1953-54 were in the Desert Shrub type (only 2 of 40 not in this type), with the bulk of these units being surrounded by the High Desert Shrub sub-type. Most of the incidentally or unused units (10 out of 16) were located in or close to a Bur-sage type, and only one (of 12) guzzlers in or adjacent to this type received as much as moderate use.

During the 3 years (1950-1953) of active and continuous Gambel's Quail studies in southern Nevada a total of 813 quail were moved from one type of habitat to another; 544 of these were released at guzzlers. Without going into detail, it can be stated that all of the transplants made to guzzlers located in or adjacent to the High Desert Shrub sub-type proved successful; the 183 quail released at these sites in 1951 to 1953 increased to an estimated 1820 birds by the summer of 1954. In contrast to this success, the release of an additional 223 quail at 4 guzzlers in poorer habitats in 1952 and 1953 resulted in populations totalling only 146 quail by the summer of 1954.

Three of these latter 4 units were located in poor Low Desert Shrub sub-types, with a uniformly poor annual food resource of the *Oenothera-Phacelia-Chaenactis-Eriogonum* group. Fifty quail (25 ♂ ♂, 25 ♀ ♀) were released at Guzzler B-1 during the desert bloom in March, 1952. By the end of the 1952 breeding season this population had increased to at least 159 birds. However, the next season failed to produce sufficient food for these birds and they numbered only 12 by July, 1953, with there being no records of quail in this area after that season.

At Guzzler N-8, 50 Gambel's Quail (26 ♂ ♂, 24 ♀ ♀) were released during the unfavorable spring of 1953 (see Fig. 2), and they failed to reproduce that season. A subsequent release of 15 quail (8 ♂ ♂, 7 ♀ ♀) was made in April, 1954, but by the end of June, 1954, the total population consisted of only 9 adults (8 were 1954 releases) and 24 young.

Although the 3rd unit, Guzzler N-11, was in a Low Desert Shrub sub-type, the presence of a long, narrow stringer of Desert Wash Shrub sub-type within 50 yards (50 m) of the unit provided habitat suitable for the maintenance of a small quail population. Consequently, the survivors from 51 quail (26 ♂ ♂, 25 ♀ ♀) released here in March, 1953, numbered 40 birds at the end of the 1953 breeding season, about 50 quail in 1954, and about 65 in 1955. Twenty-two % of the annual plants in the area adjacent to this unit belonged to the *Amsinckia-Erodium-Mentzelia* group of utilized species, providing more food here than at the 2 preceding units.

The 4th of the poorer habitats tested was at Guzzler MO-10, located in a nearly pure Blackbrush type. Fifty-seven Gambel's Quail (28 ♂ ♂, 29 ♀ ♀) were released here in April, 1953. By June, 1953, this population had dwindled to about 33 birds, and in June, 1954, it consisted of 17 adults and 36 young birds (simultaneous releases of 149 quail at 3 nearby guzzlers located in High Desert Shrub sub-type showed an increase to more than 690 quail by June, 1954). Like the 3 preceding sites, the dominant annual plant species in this area belonged to the *Oenothera-Phacelia-Eriogonum* group, plus many unutilized crucifers. However, as at N-11, the presence of a moderate number of preferred species, including *Erodium*, dwarf *Astragalus*, and *Bromus*, permitted somewhat better bird survival than at the 2 units (B-1 and N-8) where these plants were nearly totally absent.

I interpret this experimental evidence as an indication that only a limited amount of Nevada's warm desert areas will support Gambel's Quail populations, even when drinking water is readily available. Further analysis of the distribution of habitat types judged to be favorable for occupancy by this bird has shown that only about 940 of the 14,000 square miles of the Mohave Desert lying within Nevada appear to be manageable for these quail. Of this manageable area, about 526 square miles presently (as of 1954) support substantial populations. These existing populations would benefit only slightly, if at all, from additional habitat management such as the development of additional watering sites.

DISCUSSION

Gambel's Quail inhabit a considerable diversity of physical environments in the American southwest, but are confined to a rather limited type of vegetation life-form. Although there may be distinct differences between climate and the species of vegetation constituting Gambel's Quail habitat in the various areas, the life-forms of the shrubs utilized are nearly identical throughout this species' range. Schemnitz (1958), after studying Scaled Quail (*Callipepla squamata*) in Oklahoma, concluded that "The habitat of a species with a broad geographic range can be analyzed on a comparative basis more realistically when considering physiognomic units, such as life-forms, which tend to remain uniform. Taxonomic plant units tend to vary from region to region."

The *Prosopis*, *Atriplex*, *Tamarix* and *Lycium* shrub association common to the southwestern desert valleys provides a fairly uniform valley habitat for these quail from Texas west to southeastern California, southern Nevada, southwestern Utah, and northern Mexico. Altitudinal ranges are similar throughout these areas, annual precipitation is uniformly low, and winter temperatures are mild. Except for a progressive destruction of the valley habitat as more and more land goes into cultivation or other domestic uses, this environment is relatively stable. The plants which comprise this habitat are dependent upon moisture which may be derived from watersheds as much as 1,000 miles (1,600 km) distant. Valley populations of this desert quail tend to show only moderate year to year fluctuations in undisturbed habitat. Although their annual production is rarely spectacular, there is seldom a year when substantial reproduction does not occur. Population levels tend to reflect regional climatic trends.

Particularly on the western part of its range, Gambel's Quail also occurs in upland desert sites, living where a fairly uniform vegetation life-form consisting of *Acacia, Larrea, Lycium, Rhus, Yucca, Franseria*, and *Opuntia* is to be found. This hill environment is important quail habitat primarily on the Mohave Desert portions of Arizona, California and Nevada, and to a lesser extent in the southwestern parts of New Mexico and Utah. Altitudinal ranges in this situation seem to be a fairly uniform 3000 to 4500 feet (910-1370 m). Winter temperatures average well above freezing. Precipitation in these sites is normally higher than in the valleys, but still is relatively scanty (3.24-9.45 n., 82-240 mm). The hill environments are much less stable than those in the valleys, and quail populations living on these upland sites may exhibit drastic numerical changes from one season to the next. Annual bird production may vary from nothing in one year (Macgregor and Inlay 1951) to truly spectacular productivity 2 years later (Gullion 1956*b*). These birds are directly dependent upon the climate of their immediate environment. Moisture drains away from hill environments, and each season's precipitation and other climatic factors have a direct, and often disastrous bearing upon each year's brood production and population trends (Table IV, Fig. 2).

In contrast to the warm desert habitats, Gambel's Quail persist in valleys of the Colorado Basin portions of New Mexico, Colorado and Utah (where they also live in some of the valleys on the eastern edge of the Great Basin), and in north-central Idaho, in regions where winter temperatures drop well below zero (to —42°F, —41°C), and January mean temperatures are generally below freezing. The habitats occupied in these valleys are similar to one another in that *Sarcobatus vermiculatus, Chrysothamnus nauseosus, Rhus* sp., *Atriplex canescens* or *A. confertifolia,* and *Artemisia tridentata* are almost universally present. The vegetation of this entire area (except north-central Idaho) is of similar life-form, and is defined as Great Basin Microphyll Desert by Livingstone and Shreve (1921). The various climatic factors which influence the distribution of plants are similar throughout the area. Agriculture of some type is nearby, primarily alfalfa, since growing seasons in these regions are relatively short.

This seeming contradiction of an essentially warm desert bird living in regions of very low winter temperatures is resolved in the fact that the local areas occupied have amounts of precipitation within the range found on the more southerly deserts where this quail lives. In fact, annual precipitation in these colder situations averages less than at most stations within the Gambel's Quail range in Arizona and New Mexico.

Apparently Gambel's Quail living in the marginal or extralimital sites are at least partially dependent upon man's agricultural activities for survival. Both Greenhalgh in Utah (*in litt.* 1956) and Blake in Idaho (*in litt.*) include cropland as part of the habitat for the marginal or extralimital populations. It may be speculated that the increased energy available from wasted seeds (of both domestic crops and weeds) in grain fields and pastures represent the difference between existence and extinction in these areas.

The extralimital populations of *gambelii* living in the colder, more northerly localities, cannot be considered to be as secure as the populations farther south, nor as secure as the *sanus* populations farther east. Greenhalgh (*in litt.* 1955) has noted that the extralimital populations in Utah survive mild winters quite well, but drop sharply in numbers following more severe winters, and Blake (*in litt.*) indicates that the Lemhi Valley population in Idaho consists of only a few hundred birds.

It is interesting to note that the extralimital populations of *L. g. gambellii* in Utah and Idaho are living in situations which appear to be comparable with habitat of *L. g. sanus* in Colorado and northwestern New Mexico. It will be interesting to see if these extralimital populations of *gambelii* will converge towards the characteristics which separate the race *sanus* from the nominate race (Aldrich and Duvall 1955, claim that the Utah populations have already done so). Possibly transplanted populations of *sanus* might be more secure in the situations presently occupied by *gambelii* in Idaho and central and eastern Utah. There are some localities in eastern Nevada where *sanus* might prosper, and there are probably a number of other sites in the intermountain area where this cold-adapted race could become established.

SUMMARY

1. The ecology of Gambel's Quail was studied in southern Nevada, and information was gathered concerning the environment of this species in other southwestern areas.

2. Many attempts have been made to introduce this species into areas where it did not occur naturally, but success has been achieved only in a few isolated areas where the environment closely resembles the native habitat, particularly in relation to plant life-forms.

3. Although this species has a limited tolerance for the plant life-forms constituting its environment, it will tolerate a rather wide range of variation in its physical environment (such as altitude, temperature and growing seasons), so long as the area is one of deficient moisture.

4. Experimental transplants have shown that much of the desert area of Nevada (and, presumably, of adjoining states) is incapable of permanently supporting desert quail populations, even where water is readily available. This failing is primarily due to inadequate or undependable food supplies.

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PROPOSALS CONCERNING THE CONCEPT OF HABITAT AND A CLASSIFICATION OF TYPES

The use of the word "habitat" and its concept when employed as a discrete term in many of the biological sciences has become both vague and restricted during the recent expansion and fragmentation of these sciences. The term can be very useful in ecology and biogeography if all its connotations are better understood and employed. This discussion of the meaning of *habitat* and the proposed basis for a classification of the major types of habitats are presented to stimulate a more exact and a broader use of this term. Recently it has been confused with environment and biotic communities, and other expressions that designate the conditions of the surroundings of particular organisms or groups of organisms. But habitat is distinct from these because it implies more than they signify.

Habitat is often simply defined as the place where a given animal or plant naturally lives. But its meaning in the biological sciences is broader than this, and its derivation is significant. As used in English, the word was probably derived from both the Latin verb *habitāre,* (to live or dwell), and from *habit,* which is the past participle of the Latin verb *habēre,* meaning to have or hold. From these origins the word incorporates both the concept of a space or place having suitable conditions where life can dwell, and the occurrence of particular living organisms in such places and spaces.

It may be asked, must life be present for the term to apply to spaces and places suitable for a certain form of life but not occupied by the particular organism? I propose that habitats do not necessarily contain organisms or a particular organism and, consequently, there are both occupied and unoccupied habitats. I also propose that the criteria of the concept of *habitat* are distinct from those of the term and concept of environment. Before considering the full meaning of *habitat* and proposing a classification of the major types a short review of the recent literature concerning it and related terms is appropriate.

For many centuries most geographers, naturalists, biologists, and many non-scientists used the word "habitat" to designate only the location of the home of the organism considered. Sometimes they also expanded the designation of habitat to include particular conditions of the areas such as earth features, climate, associated organisms and other features. The habitats of many animals were described in terms of the vegetation or plant communities that were the usual abodes of the particular animal. The stress on climate and other conditions of the areas led to confusion with the term "environment"; this confusion will be considered first.

The term "environment" has also become confused and this has added to the vagueness of the use of both habitat and environment. Some of this confusion was discussed by Mason and Langenheim (1957) who proposed 3 components of the general environment: (1) the operational environment, (2) the potential environment, and (3) the history of environment. They considered the operational environment as most often applicable in biological sciences because it is the "organism directed" part of the general environment. They stressed that the operational environment is not the equivalent of the whole habitat and noted the difference thus: ". . . appear to have used the environment in the universal sense and habitat in the existential sense . . . habitat was considered a place in addition to conditions where a group of organisms live." This emphasis on "place in addition to conditions" significantly sets habitat apart from environment.

The use of types of vegetation and plant communities to designate the habitats of animals has led to vagueness. The plant life of an area reflects some of the conditions of the operational environment and history of environment. But the plant life of a biotic community that consists of plants, animals and other organisms is only a part of the conditions affecting most of the animals involved. Therefore, the characterization of animal habitats in such terms as rain forest, grassland, and tundra omits any characterization of the climatic and other abiotic features of the general habitat. This leads to possible misinterpretation of the conditions of the whole habitat of the biotic community.

The use of biocenotic or synecological units, such as *biotope,* to characterize habitats also has limitations, especially because the abiotic conditions are not revealed. But my stress on abiotic conditions must be qualified because in only a few cases do organisms occupy completely abiotic habitats. The majority of organisms are a part of an integrated system of abiotic and biotic components that involve matter and energy transformations which together form what has been characterized by Odum (1953) and others as an *ecosystem.* Odum defined the ecosystem as "Any entity or natural unit that includes living and nonliving parts interacting to produce a stable system in which the exchange of materials between the living and nonliving parts follows circular paths." Dansereau (1957) stated that "Within a habitat, in turn, which harbors an ecosystem consisting of one or more communities, there are other subdivisions." There are trophic levels of organisms in an ecosystem, each of which is integrated with the general habitat in a different way. The trophic and other biocenotic integrations prevail in such forms as parasitism, predation, and symbiosis.

These relationships of organisms in a small to large population or community and in small to large habitats on the earth are now being stressed by many ecologists. Thus it is becoming even less appropriate to classify animal habitats as Park (1953) did by using designations of the types of vegetation. However, Park also used marine, terrestrial and other earth features, and these abiotic designations should be generally employed.

In a recent comment Udvardy (1959) considered the concepts of habitat and the terms biotope and niche. The niche concept, he showed, is particularly useful to animal ecologists when the microhabitat of a species is considered. He also distinguished between biotope and habitat. He stated that "The concept of biotope belongs to the realm of synecology. It is a convenient term for the habitat of a biotic community. This usage should be encouraged, and certain misuse (as a synonym for habitat proper) should be eliminated."

THE CONCEPT OF HABITAT

First we will consider whether a habitat has to contain an organism to be a habitat. Can it be an abiotic place or space without life?

There are many areas and spaces where conditions are favorable for life but no life occurs in them; however, life could occur in them. An example is the lava of a volcano that becomes cool enough for life yet life may not be present because adapted disseminules have not yet migrated into the area. The blood stream of man is suitable for malaria parasites and constitutes a habitat for them before infection takes place. Other examples could be cited, such as uninnoculated culture media for particular organisms. The fact is, that if only places occupied by life are habitats it would be impossible in many cases to know when these became habitats. This would make the concept of habitat too limited. Such habitats may be considered unoccupied or potential habitats, especially those prepared for organisms such as a house for human habitation before domicile.

Such unoccupied, non-living or abiotic places and spaces are only one kind of uninhabited habitat. Another is the simple to complex biotic communities that are habitats for particular organisms. At some time such communities become adequate for another form of life which joins the complex of organisms. This occurs and is recognized in the succession of organisms in many communities. The host for parasites are also biotic habitats. They, like the abiotic habitats, can be occupied or unoccupied by particular organisms.

We will now consider the conditions and attributes of these habitats, occupied or unoccupied. First, I am arbitrarily using "place" to designate relatively fixed areas and "space" for less easily delimited areas. Geographically, habitat is used mainly to designate a place, but biologically it can be any space, such as the nose of a rocket that carries an organism into outer space. We may find that there are organisms in outer space and, if so. this vast space will be a habitat.

The main component of our concept of habitat is that the place or space must contain the resources necessary for life and that these must be available to life when necessary. These resources and requirements for life are the main criteria but are neglected or omitted in most of the concepts and uses of habitat.

The resources are various forms of energy and matter that are potentially or actively useful to the organisms. Some of the most common are light and other radiation, thermal energy, minerals, water, other inorganic matter, and organic matter. Gravity, pressure, and some electrical phenomena are also involved in most habitats on earth. A significant feature of these resources is that they are often constantly or inconstantly available; these are common conditions of light and water. This change or lack of change aspect of them is later considered to be the fundamental basis for the 4 primary categories of types of habitats. The main aspect of resources is that they must be available to the organism above its minimum requirements.

These minimum requirements of life are difficult to appraise but Allee *et al.* (1949) have outlined them as follows: (1) a set of available chemicals, including particularly water; (2) a source or sources of energy; (3) suitable temperatures, (4) suitable range of pressure; and (5) freedom from lethal diseases, toxic conditions, and harmful radiation. These conditions must be present in most, if not all habitats. I suggest that 3 additional conditions are frequently necessary. One is freedom from killing organisms that destroy some of those for which the habitat is suitable. Too many predators in some biotic communities exemplify this. A second requirement is some kind of physical support, and a third is some kind of boundary to the habitat.

A physical support is often the medium in which the animal or plant lives, as water for most aquatic life. Soil and rocks are the support of most terrestrial organisms. These are usually part of the resources, and parts of them are used in the metabolism of the organism. Air is also a support and it furnishes oxygen, but very few organisms live in the air long enough for it to be their habitat.

With the advent of rockets containing life sent into space this idea of support may become altered in situations where the condition of weightlessness occurs. It seems improbable, but it may prove true, that organisms live in space where support is not present or necessary.

Boundaries of sharp delineation are distinct in habitats such as caves, islands, and vessels containing culture media. Boundaries, whether vague or distinct, serve as protection from harmful competition by other organisms, and prevent lethal conditions from entering the habitat. The atmosphere of the earth is a boundary which prevents some radiation from reaching the biosphere.

The resources of the habitat are usually made available by the operational environment and the various activities of the organisms. For example, ice is made available as water by favorable temperature. The favorable degrees and duration of temperature are environmental factors but the water itself is a resource of the habitat. Similarly, an organism by its own external or internal activity can create heat that melts ice and makes it available as water for its metabolism. The relative levels of energy and the concentration of matter are changing or shifting in most habitats. The relative availability of most resources usually depends upon these shifts or changes. They are the factors usually considered the operational environment which is only a part of the whole habitat.

Changes and shifts in the form or concentrations of energy and matter of both the abiotic and biotic components of habitats are primarily important for the occupying life or for the potentially occupying life. Therefore, I propose that the general constancy or general inconstancy of the resources of the habitat and requirements for life can be used as criteria for distinguishing the major types. A state of absolute constancy is probably never attained, but we can recognize relatively constant conditions. The habitats with changes and shifts are of 3 main types: periodic, erratic, and sequential.

Therefore, I propose that there are 4 primary types of habitats: (1) the relatively constant, which I will term the *monotonous;* (2) the *periodic,* which generally are tidal, daily, and seasonal types on the earth (3) the *erratic,* which includes mainly habitats with sporadic or unpredictable changes, such as areas of vulcanism, fire, and some storms; and (4) the *sequential* which have changes of resources and occupying organisms in a sequence. Such changes have generally been described as a succession. This concept of the development of a successional series of biotic communities on a site applies to a few land and water areas that are abiotic habitats, but most significantly, the successions involve changes in the communities, which are biotic habitats.

The final feature to be considered about habitats is the stage or stages of the organisms occupying or potentially occupying them. Many forms of life have more than one developmental stage; some stages are active, some are dormant, and some are parts of the life cycle that need little sustenance from the surroundings. The fertilized eggs of many animals, the seeds and spores of many plants, and the pupal stages of insects are examples. These inactive stages usually do not require material and energy resources from their surroundings. Some minimum requirements for life must be present, such as a favorable pressure. But these and the operational environment can be at very low levels. Many spores, some seeds, and dormant stages of large plants can exist under conditions not suitable for their active growth stages. Therefore, I will consider habitats of particular organisms as only those places and spaces which contain or can contain life during its relatively active stage or stages.

Definition

These criteria and aspects of the concept of habitat support the following definition.

Habitats are relatively well delimited places or spaces that have sufficient resources of energy and matter to provide the necessary minimum requirements for life. They may be occupied by life, or unoccupied but suitable for occupancy by life. They are abiotic, or they are biotic communities and populations of organisms, or a single organism. The life present or capable of being present in them must be sufficiently active to obtain from the habitat some of the resources for its essential functions, if such life is to be referred to that particular habitat. The minimum requirements of life needed by the particular organism are usually made available to it through the agency of the operational environment. This environment is only a part of the habitat.

Habitats have distinct or indistinct boundaries, and they are natural or devised units of very different sizes. Many small habitats are contained within large ones. In general, biotic habitats are contained within larger abiotic habitats, and there is often an interchange of resources and requirements between these two habitats.

Places and spaces change from non-habitat conditions to habitat conditions, or vice versa. The resources, requirements, and operational environment of habitats often change and shift, or remain in a relatively steady state. The first are considered inconstant habitats; the latter, constant or monotonous habitats. These two conditions are considered the most essential criteria for a classification of the primary types of habitats.

Types of Habitats

On the basis of inconstancy compared to relative constancy of the resources, requirements for life and operational environment of habitats there are: one constant type, the *monotonous;* and 3 inconstant types, the *periodic*, the *erratic*, and the *sequential*. All 4 are proposed as primary.

The monotonous habitats are not completely constant, and many that have shifts and changes of some of the non-critical conditions can be considered as monotonous. This is the case in some tropical lands where sunlight varies with day and night, but most other habitat conditions are so nearly constant that organisms live in relative monotony of other resources and environmental factors.

The 3 types having changes and shifts do not include all that possibly occur because there may be some non-periodic but not either erratic nor sequential. Some events considered by man as erratic may be periodic, such as sun spots or severe storms. The definite periodic types are distinct in some habitats but are interrelated in others. Examples are the *tidal, daily,* and *seasonal*. The daily and seasonal are often in the same habitat.

Allee *et al.* (1949) considered periodism in detail in connection with communities of organisms. They characterized the importance of daily periodicity thus, "Within the elastic frame of seasonal rythmicity the most important periodicity is that associated with day and night. To avoid confusion in the discussion that follows, *diel* will be used for the twenty-four hour period of a night and a day." In most diels the sunlight and temperature both vary, but not in all, as during the arctic winters, and in some parts of the tropics where the variations of temperature are very small.

The nature of the erratic habitats needs clarification. Man has created many of them, in water and air and on earth, especially by fire, pollution, and now, radioactivity. He has erratically cleared forests, dammed streams, promoted floods and shaded the periodic sunlight. The biosphere now contains many more erratic habitats than before the intense activities of civilized man.

Man has also promoted certain developments toward monotonous habitats. He has built heated and air conditioned habitations and stabilized his immediate surroundings by clothing. He has made more monotonous the habitats of his domestic animals and cultivated plants, often upsetting almost entirely the previous periodicity of their habitat. In some cases the original periodicity of an organism has been altered toward monotony so that the former periodic habitat is not now required by it. In his own societies he has generally modified both his physical and social habitat toward monotony. For example, what is more monotonous for man than his armed forces with their regularity of military organization and conformity of equipment? Many habitats of cultivated fields and pastures are now so controlled that resources are completely regulated, especially in hydroponic cultivation of plants in greenhouses and in the care of poultry in large "factories."

The impact of man upon the features and resources of the earth has been forcefully considered in "Man's Role In Changing the Face of the Earth," by Thomas *et al.* (1956). These changes are only beginning and with them science will need to appraise more accurately the surroundings to identify significant differences. This need is one reason for proposing the 4 primary types of habitats, because these types fit better into a consideration of man's role than other classifications of types of habitats.

The various responses of organisms to conditions of monotony, periodicity, erraticity, and the sequential types of changes are numerous and distinct. The migration of birds and other animals and the activities of many of the tidal littoral animals are examples of responses to periodic changes. The attached and static mode of life of many organisms and the asexual forms of reproduction are prevalent in many monotonous habitats. Some trees in sequential habitats change growth forms as the succession develops. Stages of many organisms, such as seeds and spores, cysts and eggs, and the pupae of insects survive some of the critical changes of the erratic habitats.

A Proposed Classification of Habitats

The primary categories of constant or monotonous, periodic, erratic, and sequential habitats could be divided into a number of distinct secondary and lower order categories on the bases of many different earth features such as climate and biotic community conditions. But I suggest only 3 secondary categories: *aquatic, terrestrial,* and *biotic,* as most adequately discriminating. These refer mainly to the predominant media and substrata of the habitat, the aquatic to water, and the terrestrial to soil, rock and other solid media and substrata. These refer mainly to the abiotic conditions. The biotic category is the single animal host type of habitat, or the habitat is a biotic community. The medium is life surrounding the organism, populations of an organism, or mixed populations of organisms associated with the life referred to.

The selection and designation of the 3 categories is more varied and difficult, and some distinctions made by Park (1953) are used. These include factors of the operational environment such as tidal changes, day and night changes, saline and fresh water conditions, and seasonal changes. The distinctions between some of these categories are not very definite.

Many examples of places and spaces where the conditions of these respective categories occur are given in the outline below. However, these examples do not entirely conform to the conditions indicated in all instances. For example, the monotonous terrestrial, epigean habitats are given as lowland tropical areas. These areas do not have completely monotonous conditions of light and temperature but they are comparatively monotonous. There is photic inconstancy in most terrestrial habitats of the epigean subtype but the relative degrees of constancy and inconstancy of the other conditions can be recognized clearly enough to discriminate distinct types of habitats. In the examples given it may be noted that in most cases there are distinct differences. Representative animals, plants, and microorganisms living in these primary and subtypes of habitats are not given because the list would be too long.

Classification of Types of Habitats with Examples

- I. Monotonous
  - A. Aquatic
    - 1. Marine, salt and brackish water
      - Abyssal-benthic regions
    - 2. Fresh-water
      - Deep hypolimnion, deep springs, cave rivers
  - B. Terrestrial
    - 1. Epigean
      - Some lowland tropical regions, except for daily photic and thermal changes
    - 2. Hypogean
      - Subsoils and caves
  - C. Biotic
    - 1. Host
      - Warm-blooded hosts to endoparasites
    - 2. Community
      - Strata, niches, synusia of some mature, climax communities
- II. Periodic
  - A. Aquatic
    - 1. Marine
      - a. Tidal
        - Littoral zones
      - b. Daily
        - Lighted upper layers
      - c. Seasonal
        - Shallow waters of many temperate regions
    - 2. Fresh-water
      - a. Daily
        - Lighted epilimnion
      - b. Seasonal
        - Epilimnion and some hypolimnion
          - Many seasonal flooded areas, especially of rivers
  - B. Terrestrial
    - 1. Epigean
      - a. Daily
        - Most temperate land regions and some upland tropical regions
      - b. Seasonal
        - Most temperate regions, some subtropical regions, and some upland tropical regions
    - 2. Hypogean
      - Upper layers of many soils and rocklands
  - C. Biotic
    - 1. Host
      - Many animal and plant hosts to ectoparasites, and some cold-blooded hosts to endoparasites
    - 2. Community
      - Many climax plant communities of temperate and some frigid regions
- III. Erratic
  - A. Aquatic
    - 1. Marine
      - Areas of storms and rapidly shifting water currents
    - 2. Fresh-water
      - Areas of erratic flooding, and areas of erratic pollution
  - B. Terrestrial
    - 1. Epigean
      - Many areas of fires, a few areas with vulcanism, storms, avalanches, and glaciation
    - 2. Hypogean
      - Very few erratically changing caves, and glaciated areas
  - C. Biotic
    - 1. Host
      - Suddenly sick and wounded organisms
    - 2. Community
      - Many plant communities subjected to fire, some migrating animal communities, some communities being rapidly invaded by other organisms
- IV. Sequential
  - A. Aquatic
    - 1. Marine
      - Many depositional delta and shore areas, and some coral reef areas, and some eroding areas
    - 2. Fresh-water
      - Many depositional areas of rivers, lakes, temporary ponds, and some eroding areas
  - B. Terrestrial
    - 1. Epigean
      - Many depositional areas, some eroding areas, and some areas of soil development
    - 2. Hypogean
      - Developing subsoils, and filling caves

C. Biotic
  1. Host
    Developing organisms, especially organisms with stages
  2. Community
    Many successional communities

Summary

A brief review of the term habitat and the confusion of habitat with environment and other terms and concepts is followed by a discussion of the broad concept of habitat. In this discussion, it is emphasized that habitats may be either occupied or unoccupied by living organisms, that they have the resources needed for the particular life considered, and that these resources are made available to the organism through the agency of the operational environment at levels above the minimum requirements for the living processes of that organism. In considering the attributes and implications of the concept of habitat, the relative constancy and inconstancy of the essential conditions is stressed and these are selected as the basis for the primary types of habitats in a classification of habitats that is proposed. An outline of these types and the subtypes of each is presented.

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A WIND-DIRECTION RECORDER FOR REMOTE STATIONS

In 1956, a project initiated by the Research Division of the British Columbia Forest Service involved the establishment of meteorological stations at remote mountainous localities. Access to these stations was difficult, and recording meteorological instruments were employed wherever possible. Standard clock-drive instruments were available to record values of a number of climatic elements; however, the high cost of wind direction recorders, and their dependence upon a source of electricity precluded their use in this project. Consequently, efforts were made to develop a cheap wind-direction recorder requiring no electricity.

A mechanical wind-direction recorder was designed and constructed. Three of these instruments were put into operation for field testing over a three month period. The performance of these instruments has proved favourable, and the following description is presented for possible application elsewhere.

Description

Needle-arm assembly: (Fig. 1, part 1).

Two needle-arms are hinged for vertical movement in a bar (C) which turns in a horizontal plane at two pivot points provided by two screws (D) housed in a U-bar (E), which is bolted to the base of the instrument. A phonograph needle (A) is held in position near the tip of each needle-arm. Needle-arm guides (B) are mounted firmly on a flat portion of the needle-arms near the hinge end. A coil spring stretched between (C) and (F) applies tension to both needle-arms.

Cam drums and lower shaft assembly: (Fig. 1, part 2).

A coupling (H) fitted with Allen screws permits easy dismantling of the shaft for transport of the instrument. Two drums (J) with cam grooves are fixed to the shaft (I) which rides on a steel ball (K) housed in a recess in a block (G) attached to the base of the instrument.

Weather vane assembly: (Fig. 1, Part 3).

The weather vane (L), made of western red cedar, is attached to an aluminum tube which is counterbalanced with a brass plug at the tip. The vane tube is fastened to the shaft extension (O) by a screw in the weatherproof hub (N).

Shaft housing: (Fig. 1, Part 4)

A section of galvanized pipe (Q) supports and protects the extension shaft. A ball bearing (P) is mounted at the top end of the pipe and a reducer section at the lower end screws into a flange fixed to the roof of the instrument.

A seven-day clock and drum (Fig. 1, Part 5), is covered by wax-coated paper showing a weekly record of wind direction. The fully assembled instrument in a weatherproof plywood shelter is shown in Fig. 1, Part 6.

Method of Operation

The vertical shaft and attached drums rotate when the weather vane moves in response to changing wind direction. Simultaneously, the needle-arms move in a vertical plane, controlled by the needle-arm guides (B) which are held under spring tension in the cam grooves of the drums. The shape of these grooves is identical, with high and low positions diametrically opposite one another; however, the drums are offset so that high and low positions of the groove on one drum are aligned with mid-positions on the groove of the other. Consequently, when the upper needle-arm guide is riding either at the top or bottom of its drum, the lower needle-arm guide is riding in the center of its drum, and vice versa. Although both needle-arms move to indicate a prevailing wind direction, the cardinal directions are distinguished only by the extreme high and low positions;

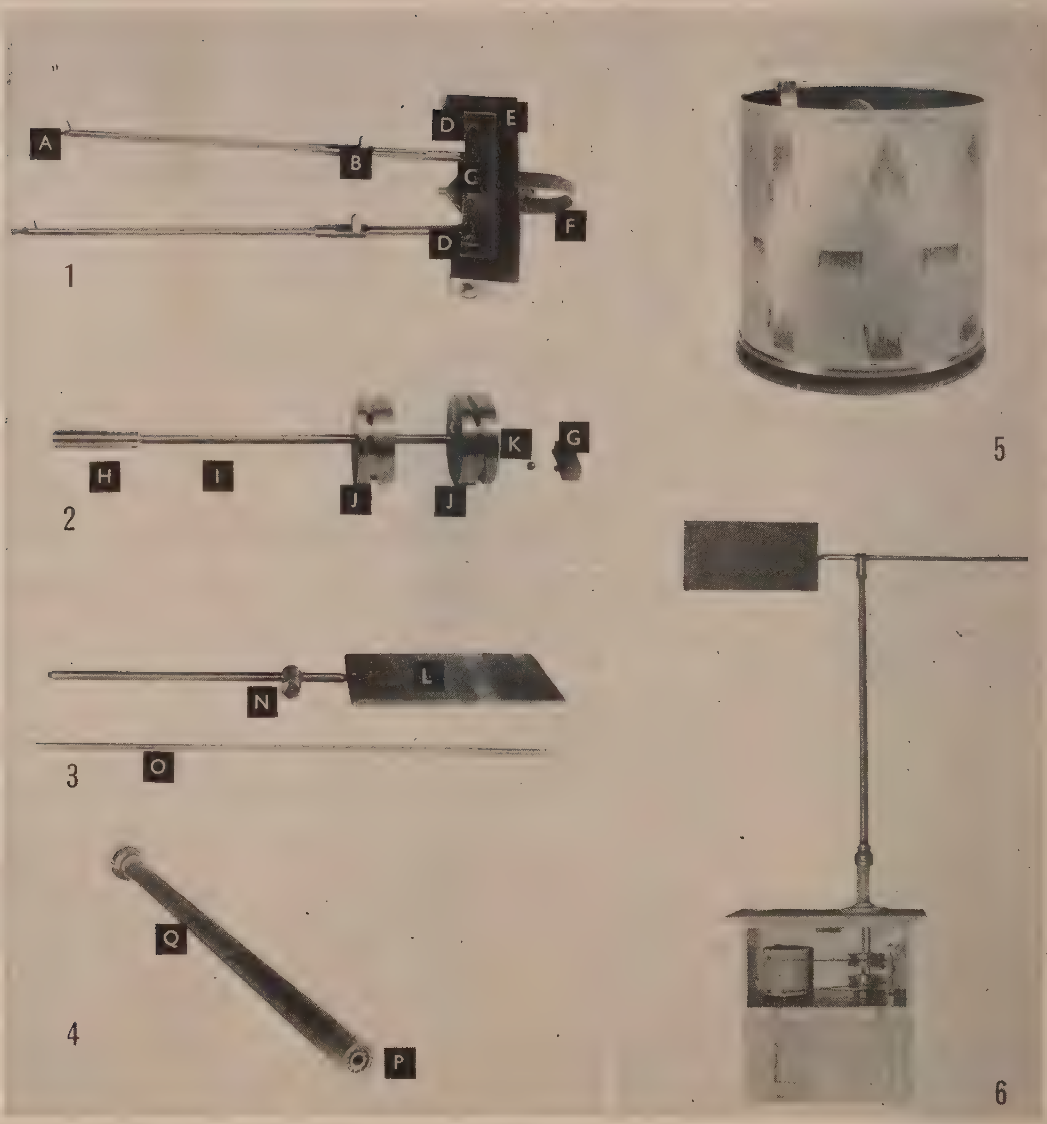

FIG. 1. Components of wind-direction recorder and fully assembled instrument.

e.g. a north wind is indicated by the upper needle at the extreme high position and the lower needle in the central position; a south wind is indicated by the upper needle at the extreme low position and lower needle again in the central position. From this example, it is evident that north and south are read only from the upper needle positions, and east and west only from the lower needle positions.

Standard thermograph pen nibs and ink were initially tried, but proved unsuccessful due to constant oscillations of the weather vane during windy periods. Phonograph needles and wax-coated coloured paper proved satisfactory. The needles scratch the wax from the paper surface, expose the coloured paper, leaving a well defined trace.

An ordinary machine shop is adequate for the production of most parts. However, a cam-cutting attachment on a lathe or a special milling machine is required to cut the cam grooves on the drums.

Throughout the design of the instrument, every effort has been made to reduce friction of moving parts, to permit recording of low-velocity winds. Friction associated with vane shaft rotation has been effectively reduced by a ball bearing at the top of the shaft, and by a steel ball supporting the shaft. Studs made of Teflon are used as needle-arm guides running in the cam grooves. (Teflon has a coefficient of friction equal to that of ice). The amount of friction applied by the phonograph needle against the chart drum can be finely adjusted, either by changing the tension of the spring or by changing set screws holding the needles in place.

The main advantages of this instrument are its suitability for use in remote localities, and economy of construction and operation. If the components are accurately machined, sensitivity of the instrument is increased to a point where even light winds of two miles per hour will be accurately traced. The instrument is now being used in connection with studies of tree pollen dispersion and seed fall over logged areas. The economy and practicality of this instrument should render it applicable to other studies where wind direction is an important weather element.

Blueprints of scale drawings and specifications are available from the authors on request. (Research Division, B. C. Forest Service, Parliament Buildings, Victoria, British Columbia, Canada).

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DEGRADATION OF POLLEN BY PHYCOMYCETES[1]

Introduction

That aquatic fungi may attack pollen became known with the publication of Braun's (1855) studies on *Rhizophydium pollinis-pini* (Braun) Zopf. Since then numerous investigators (Tomaschek 1879, Zopf 1887, Lagerheim 1890, and others) have observed that Phycomycetes destroy plant spores in nature. Zopf (1887), basing his techniques upon the efficacy of pollens as substrata for these microorganisms, developed clever methods for their isolation and cultivation. Modifications of his procedures are now routinely employed by mycologists in the study of chytridiaceous fungi (Sparrow 1943). Remy (1948) and Gaertner (1954) have demonstrated the value of plant-spore enrichment cultures in surveying the phycomyceteous flora of soil. With this technique Remy was able to demonstrate the ubiquity in soils of Rhizophydium, an organism which had previously been considered to be restricted to aquatic habitats. Her findings indicate that the distribution of this organism in the soils of Germany is comparable in extent to that of the mucors and higher fungi. As Harder (1948) has noted, by employing the proper baits it is possible to demonstrate more frequently the presence of some rarely encountered fungi. Since the pollen employed by mycologists in soil surveys has, in general, been limited to that of Pinus, it was important to ascertain the relative value of the spores of other plants. This preliminary study was made to determine (1) whether chytrids, some of which are known to degrade such resistant compounds as cellulose, chitin, and keratin (Whiffen 1941, Ajello 1948, Karling 1946, 1947; and others) may also engage in a selective destruction of plant spores; and (2) whether the use of different pollens as bait might lead to the more frequent recovery of some of the less commonly encountered chytrids.

Observations made in the course of this work are of potential interest to pollen analysts and others concerned with the destruction of pollen and spores in soils and certain aquatic environments. The agents of degradation and destruction of pollen and spores on the majority of depositing surfaces are poorly understood.

Materials and Methods

Collections were made of the top two cm of soil from 4 sites in Washtenaw County, Michigan. Each sample was thoroughly mixed and subdivided into thirty-one 10 cc portions which were dispensed into petri dishes and covered to a depth of one cm with tap water that had been autoclaved. The spores from one of 31 species of plants were then dusted over the surface of the water. The dishes were closed, covered with brown wrapping paper to retard the development of algae, and kept at room temperature.

The pollen was usually gathered by allowing the mature spore-bearing portions of the plants to dehisce on sheets of paper. However, to obtain the pollen of *Ambrosia artemisiifolia* it was necessary to macerate the flowers and to separate the grains from the resulting debris with a fine sieve. All pollen was stored in 40 cc screw top vials at 0°C in a deep freezer for a minimum of one week prior to use. The list of plants used in this study is in Table I.

The material was prepared for microscopic study by touching a sterile slide to the surface of the water in the pollen-baited cultures, adding a drop of acid fuchsin to the particles adhering to the glass, and sealing the mixture with a 20 x 40 mm coverslip. Slides were prepared daily for one month. Those slides not immediately examined were ringed with melted petrolatum and studied later. Counts of the infected spores were obtained by viewing several fields over scattered portions of the slide and observing all the grains in the sector between the "hours" of twelve and three. This process was repeated until a total of 100 grains per slide had been observed. No attempt was made to develop a more statistically valid method of sampling for this preliminary survey.

Observations and Results

Soil cultures baited with the pollen of *Zea mays, Acer negundo, Corylus americana, Populus tremuloides, P. grandidentata, P. deltoides, Fraxinus americana, Platanus occidentalis,* and *Juglans nigra* developed exceptionally rich growths of bacteria. Distinct "bacterial halos" enveloped the individual grains of these plants. However, there was no deterioration of the pollen wall that could be ascribed to the activity of these organisms. Actinoplanes (a fungus allied to the Actinomycetes) appeared on the pollen of *Pinus sylvestris, P. taeda, Picea glauca, Tsuga canadensis, Populus tremuloides, P. deltoides, Alnus glutinosa, Salix sp.,* and *Liquidamber styraciflua.* Septate mycelia formed in all the cultures but none was overgrown by these fungi (all presumably Deuteromycetes). When septate filaments invaded the grains the germ pores were the usual portals of entry.

Phycomycetes, particularly chytrids, were prominent among those microorganisms responsible for the weakening of the spore walls (Figs. 1A and 1B). These fungi appeared to be involved primarily with the contents

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TABLE I. Maximum number during one month of infections of pollen by chytridiaceous fungi per 100 grains observed

Source of Pollen	Number of Infections															
	0-10				11-20				21-40				41-80			
	Soil				Soil				Soil				Soil[3]			
	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
Zea mays				+	+		+			+						
Ambrosia artemisiifolia	+	+	+	+												
Salix sp.	+	+	+	+												
Populus deltoides	+	+		+			+									
Populus grandidentata	+	+	+	+												
Populus tremuloides	+	+	+	+												
Alnus glutinosa	+	+					+	+								
Betula pendula	+	+	+	+												
Corylus americana	+	+	+	+												
Carpinus caroliniana	+		+	+		+										
Liquidambar styraciflua		+			+		+					+				
Fraxinus americana		+	+	+	+											
Platanus occidentalis	+	+	+	+												
Quercus macrocarpa	+	+		+			+									
Juglans nigra	+	+						+			+					
Acer negundo	+	+	+	+												
Pinus sylvestris									+	+					+	+
Pinus taeda								+		+			+		+	
Pinus strobus									+					+	+	+
Pinus resinosa					+					+					+	+
Tsuga canadensis	+	+					+	+								
Pseudotsuga taxifolia										+			+			+
Picea glauca								+	+	+	+					
Picea mariana					+					+		+			+	
Juniperus sp.	+	+					+	+								
Chamaecyparis obtusa	+	+	+	+												
Ginkgo biloba	+	+	+	+												
Onoclea sensibilis	+	+	+	+												
Osmunda cinnamomea	+	+	+	+												
Equisetum arvense	+	+		+			+									
Lycopodium flabelliforme	+	+	+	+												

[3] Only soil C baited with the pollen of *Pseudotsuga taxifolia* showed evidence of more than 80 infected grains per 100 observed. In this instance an average of 94 grains per 100 were infected.

of the grains rather than with the wall material itself, although occasionally they were observed to germinate and penetrate the air sacs of coniferous spores. The smoothness of the pollen wall in the region immediately surrounding the penetrating rhizoids and discharge tubes of these organisms suggests that they digest rather than puncture the wall.

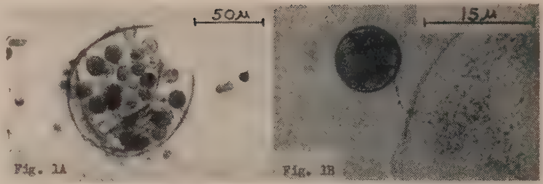

FIG. 1. A. Sporangia of Olpidium within a pollen grain of *Pseudotsuga taxifolia*. Several of the sporangia may be seen to have formed discharge tubes. B. Young sporangium of Rhizophydium on a pollen grain of *Liquidambar styraciflua*. Note that the rhizoidal system of the fungus branches within the grain.

An indication of the extent to which various pollens were attacked by chytridiaceous fungi is presented in Table I. Multiple infections were numerous and individual pollen grains were observed to bear or harbor as many as forty sporangia. The attacking chytrids were almost exclusively members of the genera Rhizophydium, Phlyctochytrium, and Olipidium, although Nowakowskiella was also associated with the grains in two of the cultures baited with the pollen of *Pinus strobus*. There was no apparent specificity for the pollens that were employed by the chytrids which invaded them; however, the pollen of *Pseudotsuga taxifolia* displayed a strikingly high number of infections by Olipidium. Several filamentous Phycomycetes, including Pythium, Saprolegnia, Brevilegnia, and Achlya developed in those cultures that had been heavily dusted with pollen.

Under the conditions employed in this study only the spores of *Osmunda cinnamomea* germinated after having been added as bait to the dishes. It is interesting that few, if any, of these germinated spores showed signs of infection by chytrids although Rhizophydium did invade the non-germinated ones (Table I). However, the use of boiled spores of Osmunda as bait resulted in a three-fold increase in the number of attacked grains.

DISCUSSION

The small number of soil samples employed in this study limits the inferences that may be drawn from the results. However, it appears that pollen grains from coniferous plants are, in general, more susceptible to decomposition by chytridiaceous fungi than are the pollen and spores of the other plants used. It is surprising that the most readily attacked pollen is that of *Pseudotsuga taxifolia*, a plant which is not indigenous to the region from which the soil samples were collected. Members of this species do, however, occur sparsely as ornamentals in the area. Similar results were obtained with some of the other pollens (*Pinus sylvestris, P. taeda*). It seems, therefore, that Gaertner (1954), in baiting his samples of African soils with the pollen of *Pinus montana*, a gymnosperm indigenous to Central Europe, was probably not unwittingly restricting either the number or type of chytrids recoverable from such samples.

The rhizoidal system of the epibiotic eucarpic chytrids ramified within the protoplasmic contents of the grains, and the entire sporangia of the endobiotic holocarpic forms developed there as well. Hence, it may be concluded that these organisms are involved primarily with the contents rather than with the walls of pollens. However, the rhizoids of the eucarpic types and the discharge tubes of the holocarpic ones appeared capable of digesting their way through the wall substance. Since there were many instances of multiple infection, such penetrations undoubtedly weaken the walls and pave the way for the decomposition of the grains by other biological agents and physical factors. Further studies on the physiology of members of genera that were among the most frequently encountered pollen attackers *i.e.*, Rhizophydium and Phlychtochytrium, are now underway. It is hoped that some insight will be gained into the characteristics of enzymes presumably responsible for the digestion of the extremely resistant material comprising the walls of pollen grains.

SUMMARY

1. Phycomycetes, particularly chytrids, constitute an important group of soil and water microorganisms engaged in the destruction of plant spores.
2. The strong tendency of these fungi to form multiple infections of individual pollen grains weakens the walls and, undoubtedly, facilitates their further decomposition by other biological agents as well as by physico-chemical forces.
3. There is variation in the extent to which pollen gains from different plants are susceptible to attack by chytrids. The spores of conifers are, in general, more readily invaded than are those from the other groups of plants tested.
4. Members of only 4 genera of chytridiaceous fungi were observed to effect degradation of pollen.
5. Pollen grains from plants indigenous to an area are not necessarily more effective as bait than pollen of exotic species for demonstrating chytrids in the microflora of that area.

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LIVE OAK AND SHIN OAK AS DESIRABLE PLANTS ON EDWARDS PLATEAU RANGES[1]

INTRODUCTION

The increase in abundance of cedar and oak on the Edwards Plateau is a problem to both ranchers and range technicians. Increase in brush has coincided with the introduction and grazing of vast numbers of cattle, sheep, and goats, increasing numbers of white-tailed deer (*Odocoileus virginianus texanus*), reduction in range fires, and severe periodic drouths. Cedar (*Juniperus ashei*) has been cleared from much of the area, but oaks (*Quercus* spp.) have often been left for forage.

The common practice of grazing cattle, sheep, and goats in common with deer appears to be the most economical means of utilizing forage production on Edwards Plateau ranges. Deer and goats, and sheep and cattle at certain times of the year, consume considerable quantities of browse. This has led to the question of the desirability of certain browse species.

One purpose of this study was to determine the desirability of oak canaopy based upon the chemical composition, productivity, density, and vigor of the associated forage species.

REVIEW OF LITERATURE

Allred (1948) concluded that some woody plants on Texas ranges are not completely troublesome or worthless unless they occur in dense stands. He reported that small amounts of live oak (*Quercus virginiana*) were desirable for forage and that post oak (*Q. stellata*), blackjack (*Q. marylandica*), and other browse plants were commonly eaten during drouth and winter periods of feed shortage.

Buechner (1944) reported that cedar is quite unpalatable even in the seedling stage to deer and stock, and that seedlings are utilized only when other feed is scarce. He concluded that stock graze more readily on oak sprouts and seedlings, and that cedar cutting encourages both oaks and grass.

Waldrip (1954) concluded that cedar should be removed from most rangelands on the Edwards Plateau since it severely reduces usable forage production. He reported that cedar is easily killed by chopping or bulldozing, but that increased forage production is assured only by good management after clearing.

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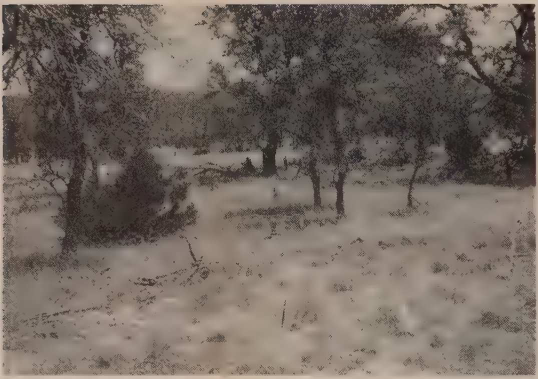

FIG. 1. Oak-grass savannah previously cleared of cedar in Kerr Co., Texas.

The Edwards Plateau is reported by Buechner (1944) to have been characterized originally by mid and tall grasses, including a predominance of little bluestem (*Andropogon scoparius*) and Texas wintergrass (*Stipa leucotricha*), and by a minimum of oak and cedar. He suggested that grazing lightly to produce climax ground cover is not as profitable as heavier common-use grazing that may produce a grama (*Bouteloua* spp.) or curly mesquite (*Hilaria belangeri*) stage in succession with moderate amounts of oak.

EXPERIMENTAL AREA AND METHODS

Physical facilities for these studies are a part of the Kerr Wildlife Management Area in Kerr County, Texas, 30 miles west of Kerrville. The Kerr Area is characteristic of much of the limestone oak-cedar savannah region of the southern and eastern extremities of the Edwards Plateau.

The present vegetation of the Kerr Area and adjacent lands is characterized by an overstory of cedar and various species of oak, including live oak, bigleaf shin oak (*Q. sinuata breviloba*), post oak, blackjack oak, and Spanish oak (*Q. texana*). These oak species grow typically in mottes giving the range a distinct savannah aspect (Figure 1). These mottes vary greatly in ground area covered, in density of canopy, and in number of stems. The vegetation understory consists of mixed grasses such as curly mesquite, Texas wintergrass, various species of threeawn grasses (*Aristida* spp.), sideoats grama (*Bouteloua curtipendula*), and others. Palatable forbs are quite scarce.

The elevation of the experimental area is about 2,200 ft. and the average annual rainfall is 28 in. Rainfall, however, fluctuates markedly from year to year. During this study annual rainfall was 18 in. in 1955, 9 in. in 1956, and 34 in in 1957. Limestone soils of the Kerr Area are mainly rough, stony, clay types of varying depth overlying bedrock.

Studies were carried out in seven 96-acre pastures. Two pastures (1 and 4) were each heavily grazed by 3 cows, 23 sheep, and 22 goats. Pastures 2 and 5 were moderately grazed by 2 cows, 10 sheep, and 10 goats per pasture. Two pastures (3 and 6) were lightly grazed each by 1 cow, 8 sheep, and 7 goats. These pastures were grazed yearlong by domestic livestock and also by a varying number of deer.

Domestic livestock were excluded from Pastures 9 and 10. Pastures 1-6 and 9 were cleared of cedar in 1939-1945. Cedar was left undisturbed in Pasture 10. Oak was not removed from any of the pastures.

Forage utilization and production were determined by the Australian difference method (McIntyre, 1946). Utilization is the difference in weight of herbage removed from a caged plot and from a paired but uncaged plot. Production is determined by subtracting the weight of forage removed from an uncaged plot at the beginning of the growth period from a corresponding caged plot at the end of the growth period. Net forage production can be positive or negative, depending on whether growth or weathering is predominant.

Sixty temporary plots were used in each pasture. To each caged plot were paired two uncaged plots. Circular plots 9.6 square feet in area were used since grams of herbage taken from this size plot, when multiplied by ten, are equivalent to pounds per acre.

Canopy cover was determined by the line transect method of Canfield (1942) with modifications. Twenty line transects 50 feet long were located in each pasture, 10 in each of two major soil types. Readings were made by visual vertical projection of canopy cover onto a 10 ft. by 50 ft. belt transect superimposed upon each line transect.

Chemical determinations of forage samples were those recommended by the Association of Official Agricultural Chemists (1955) slightly modified. Six composite samples of each species were taken at each date both under canopy and in the open. The sampling unit was the entire portion of grasses and leaves and twigs up to ⅛ inch in liveoak.

To study the distribution of herbaceous vegetation and surface rock in relation to oak canopy, 40 temporary belt transects 2 ft. x 30 ft. were established perpendicular to the edge of the canopy. Ten linear feet of each belt extended under the canopy and the remaining 20 ft. outside. Each belt was divided into 2 ft. sq. plots, in which were recorded percentage composition by area for herbaceous species and species groups and percentage area of surface rock (Brown, 1954). Field data were recorded on a degree scale and later converted to percentages.

RESULTS

Herbage Production under Oak Canopy and in the Open

Herbage production when composited from all intensities of grazing was closely related to seasonal rainfall (Table I). September-March was characterized by very drouthy conditions, while April-May rainfall was above spring normals. June-August was a period of below-average rainfall and high temperature.

During the April-May growing season sites canopied by oak produced 3.75 times as much Texas wintergrass, 1.5 times as much miscellaneous grass, 3.25 times as much total grass, and 100 times as much browse(mostly oak) as nearby open sites. Open sites produced 3 times as much forbs as canopied sites.

During the 12-month period canopied sites produced 15 times as much total grass as open sites. Although forb production in the open was almost 4.5 times as great as under oak canopy, this is less important since the forbs were annual, rather unpalatable species which dry up quickly under unfavorable growth conditions in mid-summer.

As shown in Table I, canopied sites over the 12 months produced 211.4 lbs. of available browse per acre as compared with less than .5 lb. per acre on open sites. In the late summer of 1956, following several years of drouth and heavy browse utilization, there was an average of only

TABLE I. Herbage production in pastures cleared of cedar during the 12-month period preceding September 1, 1957, under oak canopy and outside canopy. (Data in pounds per acre oven-dry)

Sites and dates	Texas wintergrass	Curly mesquite	Three awn	Miscellaneous grass	Total grass	Forbs	Browse***	Total herbage
Open site								
Sept.-March	4.5*	−19.6	−181.3*	8.1	−188.3	462.2**	.8	274.7
April-May	111.5**	33.9	− 50.3*	82.0	175.0**	642.3**	1.0	818.3
June-August	− 36.3	83.6	66.7	72.8	186.8	−404.3	− 1.4	− 219.0
Full year	85.4**	37.8	−158.3*	81.6	46.5**	705.2**	.4	751.8
Canopy site								
Sept.-March	− 62.9	−24.1	− 33.5	10.8	−109.7	263.6	13.1	167.1
April-May	418.1	26.4	42.1	116.8	603.4	217.6	138.9	959.9
June-August	46.2	15.1	72.5	10.2	143.9	−390.0	42.2	− 204.0
Full year	506.3	25.0	60.0	96.4	687.6	160.5	211.4	1059.6

* Means for open sites and similar means for canopy sites are significantly different at the .05 level.
** Means for open sites and similar means for canopy sites are significantly different at the .01 level.
*** No statistical analysis of browse data.

72.4 lbs. of browse per acre. One year later, after abundant rainfall, the average was 291.6 lbs. per acre.

Negative production figures result with the difference method when herbages losses from weathering exceed actual growth. During the Sept.-March period, a negative grass production of 188.3 and 109.7 occurred on open and canopy sites respectively.

Drouth Tolerance of Browse Species

Cedar was the browse species most tolerant of the severe 1955-1957 drouth. It lost an average of only 9.1% of its canopy. During this 2-year period cedar was able to increase by seedling growth in the pastures previously cleared of cedar at the expense of oaks. The greatest increase occurred under light stocking by cattle, sheep and goats. The respective percentage increases in cedar density under browse-line height under heavy, moderate, and light use were 7.5, 95.6, and 580%. These large differences indicate that under heavy grazing extreme starvation conditions forced browsing of some cedar regrowth.

The oak species demonstrated differences in ability to tolerate drouth. Liveoak and shin oak lost 38.7% and 45.2% of their canopy respectively. However, only 12.2% and 24.5% respectively of the liveoak and shin oak stems died. Canopy losses in the other oaks were: Spanish oak (69.2%), post oak (74.8%), and blackjack (83.7%).

Plant Distribution in Relation to Canopy and Surface Rock

The percentage composition of Texas wintergrass, curly mesquite, three-awn, and total forbs was related to canopy cover. Texas wintergrass, the most prominent forage grass producer during the 2-yr study, was most affected. Under canopy it averaged 46.1% of the herbaceous vegetation cover. However, it decreased rapidly to 21.6 and 6.3% in the first and second 10-ft segments, respectively, outside the canopy.

Relative composition of curly mesquite was 34.8% and 32.1% respectively in the first and second 10 ft segments outside the canopy. Under canopy it was only 17.6%. However, within the canopy the composition of curly mesquite increased progressively from 12.2 to 25.1% at the canopy edge.

The relative composition of purple threeawn was highly variable but attained greatest density in open areas. The component of forbs was high only in July, but the relative composition was closely related to surface rock and increased with distance from the centers of oak clumps.

The percentage of ground surface covered by rock increased with distance from the center of each oak motte. Average values for each of the three 10-ft segments along the belts were 11.8, 18.3, and 24.5% respectively. However, these percentage measurements are complicated by two factors: (1) the increased amount of concealing litter under canopy cover; and (2) somewhat accelerated erosion and subsequent increase in exposed rock on the open sites. A much greater volume of grass was produced within the first concentric ring outside the oak clumps than within the second concentric ring. This indicates that oak clumps may be exerting a favorable influence on total grass production beyond the edge of the canopy.

Curly mesquite made greater inroads into the area influenced by oak clumps on the south and west sides (the more arid sides) than on the other 2 sides. The percent composition of Texas wintergrass was much greater on the north and east perimeter of the mottes. This indicates that the oak canopy itself, apart from the soils, does exert an influence upon the distribution of these two grass species.

Chemical Composition

The protein content in both Texas wintergrass and curly mesquite was greater under canopy than in the open (Table II). This difference in protein content was highly significant (.01 level). The nitrogen-free extract and calcium tended to be higher in the grass plants not growing under canopy. Curly mesquite under canopy was materially higher in phosphorus.

The chemical composition of fully developed leaves of liveoak, a non-deciduous browse plant, did not change markedly from season to season (Table II). This was not true of the grasses. The protein content of Texas wintergrass decreased from 19.80% on April 2 to 5.69 on August 1. Phosphorus decreased from .177% to .087. Similar decreases were found associated with plant maturity in curly mesquite. These differences were highly significant (.01 level). Increases in phosphorus and protein in both grasses followed late summer rains.

When liveoak is an important constituent in the diet, it helps to maintain satisfactory nutrient levels, particularly protein and phosphorus, during summer drouths and winter dormancy. Such a role may possibly be played

TABLE II. Chemical composition of Texas wintergrass, curly mesquite, and fully developed live oak leaves

	Protein	Nitrogen free extract	Crude fiber	Phosphorus	Calcium
	%	%	%	%	%
Texas wintergrass					
Open	10.38	42.51	27.37	.121	.446
Canopy	11.17	40.86	27.25	.122	.424
Curly mesquite					
Open	8.21	43.89	27.38	.120	.382
Canopy	9.34	43.47	27.28	.131	.369
April 2					
Texas wintergrass	19.80	40.31	21.96	.177	.609
Curly mesquite	11.92	42.39	25.75	.151	.467
Live oak	8.08	51.35	26.66	.077	1.122
June 6					
Texas wintergrass	7.41	42.29	31.51	.103	.402
Curly mesquite	8.48	43.33	28.10	.134	.337
Live oak	9.57	48.25	27.54	.103	1.091
August 1					
Texas wintergrass	5.69	43.27	28.86	.087	.325
Curly mesquite	5.82	46.98	27.90	.082	.265
Live oak	8.11	47.63	27.85	.082	.899
October 25					
Texas wintergrass	10.27	40.88	26.92	.118	.404
Curly mesquite	8.89	41.80	27.58	.135	.434
Live oak	8.76	49.55	27.65	.087	1.501

to a lesser extent by cedar. The high calcium content of liveoak leaves may be undesirable in light of low phosphorus levels in the grasses.

DISCUSSION AND CONCLUSIONS

These data indicate that oak is a desirable component on Edwards Plateau ranges. The amount of oak should be regulated by adjustment in livestock numbers and classes and by mechanical methods. Too much oak greatly hinders livestock handling, limits livestock access to understory grasses, and may even decrease grass production. Too little oak lowers total forage supply and results in increased utilization of the remaining oak.

Goats and deer should remain part of a ranch livestock program where oak is prominent. Goat browsing is recommended to regulate oak densities. The oaks, particularly post oak, blackjack, and Spanish oak, often grow 15-25 ft. high and thus many leaves and stem tips are beyond the reach of grazing animals. It may be necessary to fell oak periodically to make the forage available.

Shin oak and live oak appear more desirable than other oaks, even though post oak, blackjack, and Spanish oak may be as palatable. Shin and live oak tend to be lower growing, heavier sprout producers, and more drouth resistant. There is also evidence that taller oaks may produce such dense overstories that they actually reduce herbaceous forage production beneath. It may sometimes be desirable to remove the 3 taller oak species when cedar is cleared.

Areas cleared of cedar produced 6.5 and 2.0 times as much total grass on open and canopied sites, respectively, as where no cedar was cleared. This indicates that cedar canopy differs from oak canopy in severely competing with grass and greatly limiting grass production.

It has been experimentally demonstrated and commonly observed that a smaller percentage of the plants are climax decreasers in areas cleared than in those not cleared of cedar. This may be a result of opening up cedar areas for more complete grazing by livestock. Non-cleared areas produce more climax decreaser plants but much less total grass herbage. For maintenance of a component of climax decreaser plants it will probably be necessary to restrict grazing during the first year or two following cedar clearing, and graze lightly thereafter.

SUMMARY

Studies in Kerr County, Texas, determined the relative desirability of oak species on southern Edwards Plateau ranges.

Sites covered by oak canopy produced significantly more Texas wintergrass, threeawn, and total grass, but significantly fewer annual forbs than open sites. Total herbage production on open sites amounted to only 71% of that produced on canopied sites. In addition, 72.4 and 291.6 lb per acre of oak browse were available for livestock consumption on canopied sites in the late summers of 1956 and 1957, respectively.

Grasses on canopied sites contained significantly more crude protein but somewhat less nitrogen-free extract than grasses growing on open sites. It was concluded that, where oak occurred in open stands that did not greatly restrict livestock grazing, beneficial results were obtained from browse production and greater grass production.

It was concluded that cedar should be cleared where feasible because of its low palatability, severe competition with grasses, and hindrance to livestock handling.

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ECTOTROPHIC FOREST TREE MYCORRHIZAE AND FOREST COMMUNITIES[1]

This study deals with ectotrophic and endectotropic mycorrhiza of forest trees and their herbaceous and shrub-like relatives. This type of mycorrhiza is morphologically and physiologically defined, and the definition is further strengthened by the fact that the organisms participating in this complex relation belong to a fixed list of genera which are ectomycorrhizal, both on the fungus and the cormophyte side (see list, p. ..). Therefore we should expect a traceable area of distribution of mycorrhiza of this type, an area which should roughly coincide with the respective combined areas of its components. The authors are now preparing a world map showing this coincidence of ectotrophic forest tree mycorrhiza with the combined areas of its components. The area includes the temperate zones of the northern hemisphere, parts of the subtropical and tropical zones of the northern hemisphere (where Pinus or Quercus or both form a forest climax) and the frigid zone to and often beyond the tree line. In addition, it includes the entire Nothofagus area and a narrow montane line stretching from Mexico southwards along the Andes, consisting of Alnus. Outside these limits are merely isolated islands of Salix mycorrhiza, particularly along the rivers, and cicatrizer mycorrhiza which is discussed below. Mycorrhiza introduced with seedlings outside the natural area of the mycorrhiza trees is not taken into consideration. Inside these limits, mycorrhiza is absent mainly in some parts of the large desert regions of Asia and North America.

We shall take the majority of our examples from South America since this is the region with which we are best acquainted. In other parts of the world, some modifications may be necessary, particularly in altitudinal zonation studies, but we believe our results have a worldwide application. Yet, some points, even in the Americas, still need further study. For example, we do not fully understand the native ectotrophic mycorrhiza of *Salix humboldtiana* since it is impossible to ascertain whether the two mycorrhizal fungi *Alnicola devia* Sing. and *Hebeloma sacchariolens* Quél. were introduced with European willows or other trees and later invaded the stands of native species. There is also still some doubt about the regularity and the role of ectotrophic mycorrhiza on Californian Sequoia.

In South America, we have three ectotroph regions (the composite organism which is comparable to a lichenized fungus, both physiologically and ecologically, consisting of tree-mycorrhiza-fungus and corresponding to the definition given in the introductory paragraph, is referred to as *ectotroph*):

(1) The small *Quercus* area in Colombia which is believed to be a continuation of the large Central American ectotroph complex with oak participation, and which is mycologically unexplored.

(2) The South American extension of the area of *Alnus jorullensis* along the Andes, reaching the Argentine province of Catamarca in the south. One of the characteristic ectotrophs of the area is *Alnus jorullensis/Gyrodon monticola* which reaches from Mexico to Argentina. The fungus component may be replaced by species of Russula, Lactarius, Cortinarius, Alnicola, Inocybe.

(3) The largest and most important ectotroph area south of the northern hemisphere: the Nothofagus region with two typical representatives, *Nothofagus dombeyi/Russula major* and *Nothofagus pumilio/Russula nothofaginea*. Both tree and fungus are replaceable by numerous other mycorrhizal partners. Particularly interesting is the ectotroph combination *Nothofagus dombeyi/Boletus loyo*. These southern ectotrophs find their natural geographical continuation in the Nothofagus areas of New Zealand, Australia, New Caledonia, and New Guinea.

Beyond these areas of complete coincidence of the natural area of cormophyte and fungus component, human activity makes possible the existence of ectotrophs of the type *plantation tree/adventive fungus*. The cormophyte here is mostly Pinus, Quercus, Populus, Salix, Larix, Cedrus, Betula, Alnus. The fungi are mostly of European and North American origin.

There are cases of complete coincidence of cormophyte and fungus area in a given ectotroph, as with *Alnus jorullensis/Gyrodon monticola*. In other instances the coincidence is distinctly incomplete because of different adaptability and migration capacity of fungus and tree as in *Nothofagus dombeyi/Boletus loyo*. Here, the fungus is replaced by others wherever the tree advances outside the typical Valdivian floral district. *Boletus loyo* is a snow-injured species which does not survive or fruit in areas covered by snow in winter.

We can also distinguish between stable elements which accompany the tree only in its native area, and others whose adaptability makes it possible to appear as adventive elements in plantations. An example of the stable union is *Pinus silvestris/Suillus flavidus* and of the adaptable one: *Pinus silvestris/Suillus luteus*.

We believe that the comparison of ectotroph communities with communities lacking ectotrophs in the climax has considerable importance in the study of forest communities and can provide answers as to the mechanism that determines their present distribution. In the following paragraphs, we shall discuss a few aspects this new approach suggests.

The ectotroph as a biological unit generally possesses higher plasticity than any comparable forest element without mycorrhiza. In an association, the ectotroph is usually the element with the highest fidelity and regularity of distribution, and is commonly the first to establish itself among its consociates. The distribution of mycorrhizal dominants and subdominants of this type shows an even distribution throughout the stand which causes the ectotroph mycelium to occupy the soil almost homogeneously (for example in mixed mycorrhizal and non-mycorrhizal associations in Florida, Southern Mexico, and Southern Chile). Fidelity and regularity may be explained by tropic reasons favoring the ectotroph over the non-mycorrhizal element and making it more aggressive and often more resistant to unfavorable climatic conditions and to diseases.

A completely mycorrhizal community is characteristic of strongly contrasted thermoperiodical climates and is found in the high mountains of South America except where excessive dryness inhibits the development of an ectotrophic mycelium.

The development of ectotrophs is limited by two main factors:

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[1] Communication read by the senior author at the IX International Botanical Congress at Montreal. Paper from the Departmento de Botánica, Instituto Miguel Lillo, Tucumán, Argentina.

(1) Dryness. In South America there are no xerophytic or semixerophytic forest communities with ectotroph elements. It is true that Quercus and Pinus often take part in near-xerophytic associations in the northern hemisphere; however, the southward migration of Pinus ends in Central America and that of Quercus in Columbia. Larix, also part of semi-xerophytic associations in Asia, does not come near the continent of South America. Furthermore, a characteristic adaptation to the soft deep Chaco soil with its limited precipitation is the development of vertical roots which are not compatible with the formation of ectotrophic mycorrhiza.

(2) Humidity (if accompanied by generally high temperatures throughout the year and absence of deep absolute lows). Under these conditions mycorrhizal types other than the ectotrophic forest mycorrhiza are better adapted to take over; they are less dependent on the water in the soil than that of the host tissue and cell interior. Under these conditions elements with endotrophic mycorrhiza (bacterial, actinomycetal and fungal) predominate.

In very humid climates with relatively low temperatures, however, ectotrophs are common, as in Southern Chile, but the frequency and abundance of species increases passing from a humid isothermic to a humid heterothermic clima. This is in accord with the further observation that in the incomparably richer flora of the Valdivian forests there are fewer species of mycorrhiza formers in the fungi than there are in the drier and more thermoperiodical Argentine (eastern) part of the Nothofagus zone.

In the intratropical and subtropical zone of South America ectotrophs are known exclusively in regions with strong thermoperiodicity, *i. e.* in the montane zone. The same is true for the subtropical zone. Where the thermoperiodicity is still noticeable though less pronounced, ectotrophs are absent in the forest climax, both in the basal subtropical forest and in the leaf-shedding pre-montane forests.

Similar situations are evident in New Zealand (Agathis-Beilschmiedia vs. Nothofagus woods).

We do not mean to imply that ectotrophs are completely absent in the less thermoperiodical regions of the neotropics and subtropics. We have observed that in the subtropical zone (and this may also apply to the tropical zone) ectotrophs are found as cicatrizers or nomads. They play exactly the same role as the ectotroph *Pinus merkusii/Suillus* aff. *bovinus*[2]) in the Philippines and North Sumatra and as other pines with respective mycorrhiza in parts of India (Puri and Van Steenis, 1956). These pines are generally difficult to establish in nurseries outside their natural area without mycorrhiza innoculation (generally with mycorrhiza-bearing forest litter) as has been reported from Australia, Africa, the East Indies, and the Atlantic Coast of North America. The characteristic South American cicatrizer ectotroph is *Allophylus edulis/Gyrodon rompelii.* This union may temporarily dominate some stage of the succession in second growth forest where landslides, fires, or selective wood cutting have upset the climax vegetation. This suggests that in the subtropical and probably also the tropical zone, ectotroph dominance occurs only in seral communities, and mainly in the role of cicatrizers or nomads. Cicatrizers are generally mycorrhizal in one way or another.

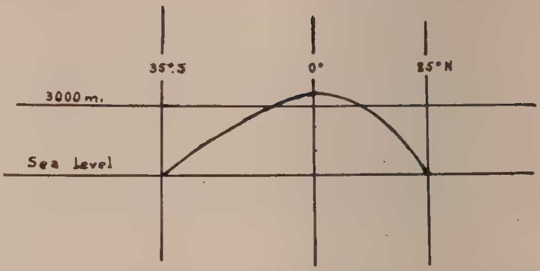

FIG. 1. Approximate dividing line between ectotroph forest and non-ectotroph forest under non-xerophytic conditions (see text).

On a strongly schematized profile of the Americas we could draw a curve, on the basis of these observations, which would form a somewhat imperfect yet not irregular arch starting at sea level in south Central Chile, culminating above 3000 m near the equator and reaching sea level again at approximately 20° N. This curve divides the predominantly ecto-mycorrhizal from the predominantly non-ectomycorrhizal forests, the latter falling below the curve and the former above and outside it. This, naturally, is valid only within the limitations indicated above for the existence of ectotroph forest —and forest generally, *i. e.* not considering interruptions in the continuity of the forest cover by Puna, natural pampa, desert, etc. (Fig. 1).

One problem left for future investigations is the role of the endotrophic mycorrhiza as compared with that of the ectotroph. It seems to us that as a natural biological unit endotrophic mycorrhiza is not a meaningful term and cannot, therefore, be evaluated as an important tool of the forest ecologist. It is evidently up to the physiologist, forest ecologist, mycologist and taxonomist to provide us with a natural rather than purely morphological grouping of phenomena now generally combined in the term endotrophic mycorrhiza. In order to be comparable with the ectotroph, the analogous endotrophic complex organisms would have to be classified. It is already doubtful whether the widely accepted disregard for the identity of the symbionts in mycorrhiza is an attitude useful for the physiologist; it is certainly an attitude barring progress in ecology.

SUMMARY

The biological unit forest tree/ectotrophic mycorrhiza /fungus (the *ectotroph*) occurs as dominant or subdominant in climax forests in three areas of South America but is widely distributed as cicatrizer outside these areas. Its occurrence is determined by definite ecological and climatic conditions.

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LIST OF THE ECTOTROPH COMPONENTS

1. Cormophyte components of ectotrophs:

Pinaceae: *Pinus Tsuga, Pseudotsuga, Abies, Picea, Larix, Cedrus*
Salicaceae: *Salix, Populus*

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[2] This fungus is generally determined as *Boletus bovinus.* It is, however, probable that it is a species closely related to *Suillus bovinus,* but not identical.

Fagaceae: *Fagus, Nothofagus, Quercus,* and allied genera, *Castanea.*
Betulaceae: *Betula, Carpinus, Ostrya, Alnus, Corylus*
Oleaceae: *Fraxinus*
Sapindaceae: *Fraxinus*
Leguminosae: *Inga*

2. Fungous components of ectotrophs:
Agaricales:
  Hygrophoraceae: *Hygrophorus* sensu stricto
  Tricholomataceae: *Tricholoma* (without sect. *Contextocutis*), *Porpoloma* subg. *Porpoloma, Catathelasma*
  Amanitaceae: *Amanita* (without sections *Strobiliformes* and *Roanokenses*)
  Cortinariaceae: *Inocybe, Hebeloma, Alnicola, Descolea, Rozites, Leucocortinarius, Cortinarius.*
  Paxillaceae: *Paxillus* p.p. (species of *Nothofagus* area)
  Gomphidiaceae: *Gomphidius,* probably also *Cystogomphus*
  Boletaceae: *Phylloporus* (?). *Xerocomus* (not all species), *Boletinus, Suillus Psiloboletinus, Paragyrodon, Gyrodon, Pulveroboletus, Boletus, Tylopilus, Xanthoconium, Leccinum.*
  Russulaceae: *Russula, Lactarius*
Gastromycetes (Lycoperdales)
  Secotiaceae: *Macowanites, Thaxterogaster, Gastroboletus, Truncocolumella*
  Rhizopogonaceae: *Rhizopogon* and perhaps some related genera.
  Sclerodermataceae: *Scleroderma* and *Pisolithus* (mycorrhiza perhaps not typical)
Aphyllophorales (Cantharellales):
  Pore-bearing: *Scutiger, Boletopsis.*—Spine bearing (hydnaceous): *Sarcodon,* and related genera, *Hydnum repandum* and allied species (*Dentinum*).—Clavarioid: *Clavariella* (*Ramaria*), *Clavariadelphus*—Cantharellaceous: Cantharellus, Craterellus, *Gomphus,* probably *Polyozellus* and *Gloeocantharellus.*

AN INDEX TO THE RATE OF CELLULOSE DECOMPOSITION IN THE SOIL[1]

In terrestrial ecosystems a large portion of the net primary production may be channeled to the decomposer organisms. For example, in the bluegrass old field community it has been estimated that decomposers may use 70% of the net production (Golley 1958). However, we have little information about the structure of decomposer food chains and the rate of decomposition of organic materials. This note reports preliminary results of measuring rates of cellulose decomposition in various soils.

The technique used was modified from that described by Tribe (1957) for studying succession of soil microorganisms on cellulose sheet. The method involved placing a square of cellulose 5 x 5 cm between a folded rectangle of aluminum screen and placing the screen and cellulose vertically in the soil, the upper edge at the soil surface. Pure, regenerated cellulose was used—this was entirely alpha cellulose with approximately 6-7% water[2]. Tribe reported that he affixed cellulose to glass slides by wetting it before placing it against the glass. I was unable to do this and was informed by E. I. Dupont de Nemours & Company that a special bonding agent would be necessary to cement cellulose to glass. The aluminum screen may have influenced the soil organisms in some way, but since all strips were treated alike, this does not invalidate the comparative data. After a certain time the strip was removed from the soil and an estimate was made of the rate of cellulose breakdown by computing the remaining area of the original sheet.

Cellulose strips were placed in the soil at the Savannah River Plant, Aiken County, South Carolina, in February, 1959. Three sites were chosen for study. First, strips were placed at a site with very little vegetation, mainly *Andropogon virginicus* (termed light broomsedge site). Here the cellulose was placed in bare sand approximately 50 cm from the nearest vegetation. Second, on an area with medium cover of *A. virginicus,* strips were placed in sand within 10 cm of broomsedge clumps. Finally, on an area with very dense *A. ternarius,* strips, were placed in rich, black sand-loam, at the base of broomsedge clumps. Later strips were also placed under loblolly pine (*Pinus taeda*) and turkey oak (*Quercus laevis*) litter.

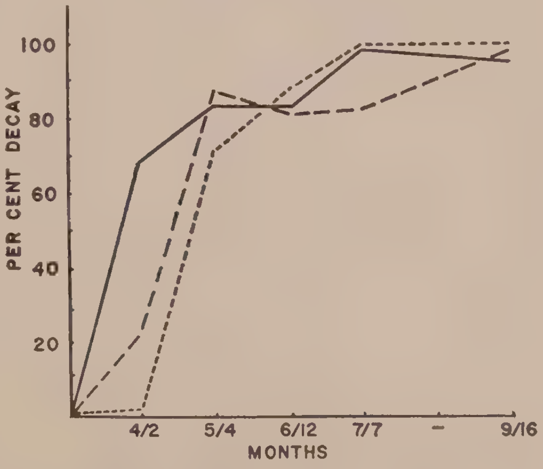

Fig. 1. The per cent decay of cellulose sheet in three vegetation types. Light broomsedge (solid line), medium broomsedge (heavy-dashed line) and heavy broomsedge (light-dashed line).

Each month three of the original set of cellulose strips placed in the soil in February were removed and the progression of decomposition noted (Fig. 1). The rates of breakdown were approximately the same in the 3 types of broomsedge, although decomposition appeared to be initially delayed in the heavy stand of *A. ternarius.* Almost 90% of the strips had decomposed by the 4th month and by the 6th month practically all the cellulose was gone.

Each month new cellulose strips were placed in the ground at the 3 sites to determine initial decay rates (Fig. 2). During the spring, the per cent of cellulose breakdown in one month continued to increase. Decay

[1] This research was supported by the U. S. Atomic Energy Commission (Contract At(07-2)-10).

[2] The cellulose was kindly supplied by E. I. Dupont de Nemours and Company, Wilmington, Delaware.

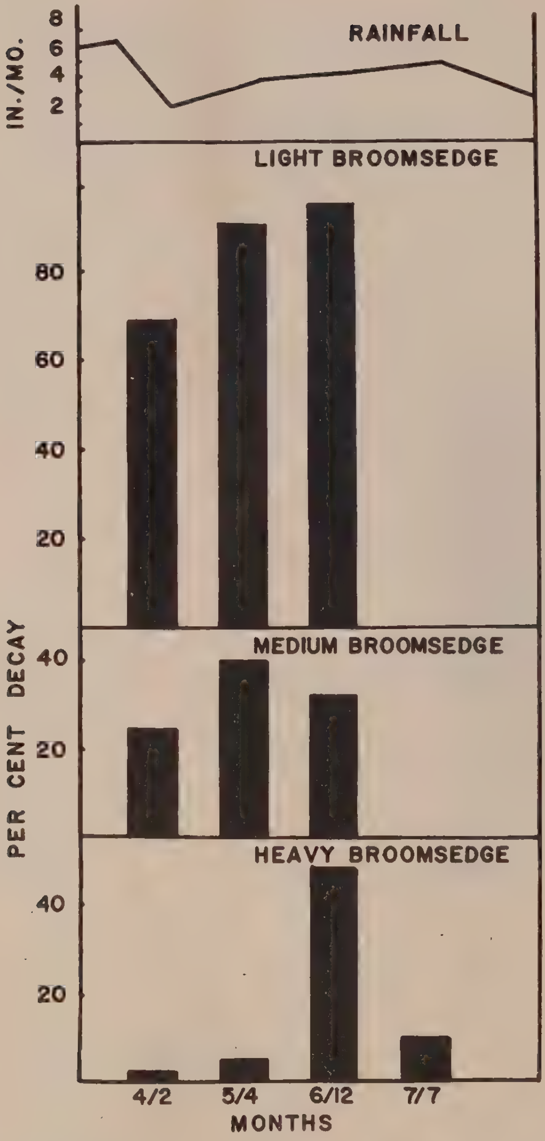

Fig. 2. The per cent decay of cellulose sheet in one month during late spring and early summer.

was most rapid in bare sand and slowest in the heavy stand of broomsedge. In early summer (June 12-July 7) cellulose decay almost stopped in all the broomsedge sites and in the pine and turkey oak sites. Decay began again in late summer. Cellulose placed in the ground in July and examined in September showed 24% decay in light broomsedge, 46% in medium broomsedge, 91% in heavy broomsedge, 65% in pine and 91% in turkey oak.

In addition to the South Carolina sites, cellulose was placed in soil in the montane rain-forest, Puerto Rico, for three weeks in May, 1959, and in the spruce-fir forest and alpine tundra, Medicine Bow Mountains, Wyoming, for the month of August, 1959. In each site 6 strips were placed in the ground and 4 were laid horizontally on the soil surface under leaf litter. Almost no decomposition was recorded at these sites. The rain-forest strips in the soil showed less than one per cent decomposition. Other sites showed no decay.

Although the number of observations are limited, certain notable trends appear. First, at the Savannah River Project complete decomposition of cellulose occurs in 6 months. This is a rather rapid rate of decay but is not unreasonable, since field observations indicate that broomsedge leaves on the soil surface disappear in approximately this time. Large stems of herbs, such as Heterotheca, do not break down rapidly, however; some of these may last 6-7 yr on the soil surface.

Second, decay rates increase during the spring and decay ceases abruptly in mid-summer. Fungi are the first organisms to attack cellulose (Tribe 1957), followed by bacteria. Thus Fig. 2 indicates the rate of fungus-caused decay. Increase in decomposition during the spring may be related to the rise in temperature during this period—increase in temperature speeding up the activity of decay-causing fungi. Abrupt cessation of decay in July may be thought to be caused by drought conditions common during mid-summer on the coastal plain, but rainfall data (Fig. 2) indicate this is not so.

Third, the rate of decay during the first month is more rapid in bare sand than in sand-loam. This high rate of decay in the light broomsedge site might be due to a higher fungus population in bare sand, or to the absence of other cellulose in the bare sand which might act as a "buffer" to the cellulose strip. Apparently there is some factor in the heavy broomsedge that is uncongenial to fungal development. After the second month decay rates in heavy broomsedge, resulting from bacterial action, are similar to those in light and medium broomsedge sites.

I am unable to explain the absence of decomposition of cellulose sheet in the rainforest, spruce-fir forest and in the alpine tundra. In the tropics cellulose decomposition is supposed to occur very rapidly and we would expect the greatest decay to have been in the rain-forest site. In the spruce-fir forest and alpine tundra decomposition is greatly reduced because of low temperatures. Yet we would expect some breakdown of cellulose during the late summer, especially under the seemingly fungus-rich spruce litter.

The lack of success of measuring rates of cellulose decay in the rain-forest and in the spruce-fir and alpine tundra indicates that the cellulose strip method is not effective under all conditions. In ecosystems where the method does give definite results, as in South Carolina, the cellulose strip technique has value as an index to the activity of the decomposer levels of the community.

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PHYSIOGNOMIC INTERGRADATION OF VEGETATION ON THE PINE VALLEY MOUNTAINS IN SOUTHWESTERN UTAH[1]

INTRODUCTION

The Pine Valley Mountains are located in Washington County in extreme southwestern Utah. They reach a maximum elevation of well over 10,000 feet, and the vegetation exhibits a wide range of physiognomy, from boreal forest down to desert shrub.

If floristic combinations (associations) within a given physiognomic vegetation type (formation) intergrade continuously (Curtis and McIntosh 1951; Whittaker 1952, 1956), what is the nature of the intergradation between formations with widely different physiognomy? The present vegetation analysis was undertaken in an attempt to elucidate this question.

The upper few thousand feet of these mountains consists of an erosion-resistant igneous intrusion of andesite-porphyry; this rests on a thick series of sedimentary strata ranging from Eocene limestone down to Triassic sandstones and shales. Sloping away from the east side of the mountains as a widespreading graded sheet is a coarse alluvium, characterized by large porphyry boulders; it varies from a thin veneer on the bedrock to terraces 100 or more feet thick. The present streams have trenched the alluvial apron, leaving the remnants in interstream divides several hundred feet above the present stream bottoms. Since this alluvium extends continuously from desert elevations upward, it affords a reasonably constant substratum on which to examine the vegetation gradient correlated with elevation, with some hope for a linear ordination.

On the southeastern side of the mountains, this gradient was sampled at 15 points at altitudinal intervals of about 250 ft, ranging from an elevation of 3,000 ft near Harrisburg to 6,250 ft near Oak Grove Camp at the head of Leeds Creek. Sampling was done by a point-centered quarter method (Cottam and Curtis 1956). The distance from the center to the nearest shrub was measured in each quadrant; the mean distance squared is the mean area per shrub (reciprocal of density). In addition, the two next nearest shrubs in each quadrant were recorded, giving a total of 12 shrubs per sampling point. Ten random points along a transect were taken at each elevation, providing a sample of 120 shrubs. All sampling was done on bouldery alluvium without appreciable slope exposure.

If the vegetational gradient were described only in floristic terms, it would be possible to convey a dim picture of some of the obvious physiognomic features. A clearer conception of the vegetation may be obtained by grouping the dominants according to their physiognomy. Hence, the following physiognomic classification will be adopted:

1. Microphyllous Shrub Formation: mostly evergreen.
   (Sonoran Desert Shrub)
   Larrea tridentata[2]
   Franseria dumosa
   Krameria parvifolia (parasitic on roots of above spp.)
2. Microphyllous Shrub Formation: mostly deciduous
   (Mohavean Desert Shrub)
   Coleogyne ramosissima
   Haplopappus linearifolius
   Lycium andersonii
   Acamptopappus sphaerocephalus
   Hymenoclea salsola
   Ephedra nevadensis
   Dalea Fremontii
   Prunus fasciculata
   Tetradymia spinosa
3. Evergreen Pygmy Tree Formation
   (Pinyon-Juniper Woodland)
   Juniperus osteosperma
   Pinus monophylla
   Cowania mexicana
4. Evergreen Broad-Sclerophyll Shrub Formation
   (True Chaparral, floristically similar to the Arizona Chaparral)
   Quercus turbinella
   Ceanothus Greggii
   Arctostaphylos pungens
   Garrya flavescens
   Cercocarpus ledifolius
   Eriodictyon angustifolium
5. Broadleaf Deciduous Woodland Formation
   (Elements of Clements' Petran Chaparral)
   Quercus gambelii
   Amelanchier utahensis

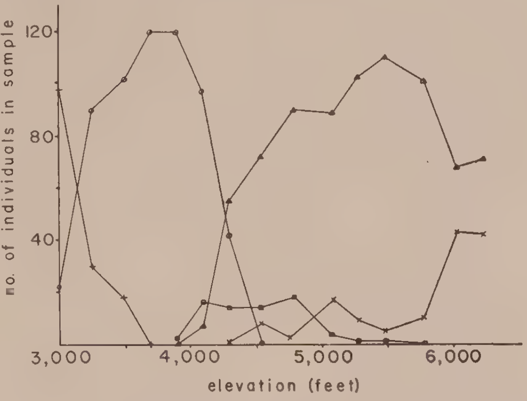

FIG. 1. Variation in physiognomic composition of the vegetation with elevation. The numerical proportion of each of the five major physiognomic types is plotted against elevation. This is based on a sample of 120 individuals at each elevation investigated.

Legend: +, evergreen microphyllous shrub (*Larrea-Franseria*). Circles, deciduous microphyllous shrub (Coleogyne). Triangles, evergreen broad-sclerophyllous shrub (chaparral). Squares, evergreen pygmy tree (pinyon-juniper). X, deciduous broadleaf tree or tall shrub (oak-woodland).

RESULTS

In Figure 1 the number of individuals in each physiognomic group is plotted against elevation. Starting at 3,000 ft the evergreen shrubs dominate strongly, but there is already an infusion of a more temperate deciduous element, principally the rosaceous Coleogyne. Two synusiae are conspicuous; the taller (1 to 2 m high) bronze-green Lar-

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[1] Field work was supported in part by National Science Foundation Grant 3834.

[2] Nomenclature used in this paper follows Kearney and Peebles (1951).

TABLE I. Total number of individuals of each species at each sampling elevation. Sample size, 120 individuals.

	ELEVATION (in feet).														
	3000	3250	3500	3700	3900	4100	4300	4550	4800	5100	5300	5550	5800	6050	6250
Franseria dumosa	50														
Krameria parvifolia	25	4													
Larrea tridentata	23	26	18												
Coleogyne ramosissima	16	43	88	84	108	76									
Lycium andersonii	4	3													
Dalea Fremontii	1	7	2												
Ephedra nevadensis	1			1											
Hymenoclea salsola		31	10												
Chrysothamnus pulchellus		2	2	1	1										
Acamptopappus sphaerocephalus		2													
Haplopappus linearifolius		1		26	8	15	38								
Prunus fasciculata		1		1	1	2									
Gutierrezia microcephalus				7			2						2		
Purshia tridentata					1										
Tetradymia spinosa					1										
Juniperus osteosperma						9	11	10	16	1					
Quercus turbinella						7	24	59	57	41	47	40	17	8	2
Cowania mexicana						6									
Opuntia tenuispina						3									
Opuntia erinacea						1									
Pinus monophylla						1	3	4	2	2	1	1			
Ceanothus Greggii							26	6	23	6	18	21	45	11	8
Artemisia tridentata							7	26	8	11	7	4	7	9	7
Arctostaphylos pungens							4	2	6	9	12	17	32	2	2
Opuntia rhodantha							2								
Ephedra viridis							1								
Garrya flavescens							1	5	4	30	26	32	7	45	43
Amelanchier utahensis							1	8	2	6	9	5		28	22
Yucca baccata									1						
Opuntia aurea									1						
Quercus gambelii										11			10	15	20
Eriodictyon angustifolium										3					
Cercocarpus ledifolius														2	16

rea shrubs are scattered orchard-wise in the open matrix of the gray dwarf shrub synusia (ca. 0.5 m high). With increasing elevation, the taller Larrea synusia is eliminated and the dwarf shrub layer is increasingly dominated by Coleogyne. At 3,700 ft, the vegetation is a monotonous dark gray expanse of dwarf shrubs, almost a pure stand of Coleogyne. When wet following a shower, it has a very dark appearance; hence the local name black brush.

At 4,100 ft, a very open synusia of evergreen pygmy trees (junipers ca. 2 meters high) is scattered over the Coleogyne. Outlier junipers range to lower elevations, overlapping the upper range limits of Larrea. Also at 4,100 ft, the chaparral or broad sclerophyll element is represented by scattered bushes of the holly-leaved *Quercus turbinella.* Between 4,100 ft and 4,300 ft a transition takes place in the shrub synusia from deciduous microphylls about 0.5 m high to evergreen broad sclerophylls 1 to 2 m high (chaparral). The pygmy tree synusia remains about the same throughout this change except that the trees become taller at the higher elevation. Then, at about 5,000 ft, the open synusia of junipers and pinyons drops out and a scattered element of broad-leaf deciduous trees or tall shrubs (chiefly *Quercus gambelii;* 2 to 3 m high) makes an appearance in the matrix of evergreen chaparral. Above 6,000 feet this deciduous element increases and shares the dominance with the evergreen sclerophylls, but both are soon subordinated to the status of open underwood in the *Pinus ponderosa* forest which prevails above 6,500 ft. This forest was chosen as an upper limit in the present study.

The sampling data are presented in terms of individual species in Table I. In the treatment by physiognomic classes, *Artemisia tridentata* and several of the more infrequent species were omitted. On this side of the Pine Valley Mountains, sagebrush is a ubiquitous weed on every small cattle trail, usually in dwarfed form; hence its presence is no more significant than the ruderal herbs, which were not sampled.

The sampling method employed affords a measure of the mean area per plant, which is the reciprocal of the absolute density. In Figure 2, mean area per plant, expressed in square meters, is plotted against elevation. Paradoxically, the open desert vegetation proves to have the greatest density (smallest mean area per plant), while the closed stand of chaparral has the least density. Although the chaparral shrubs are more widely spaced, the individuals are large and extensively branched, providing a much greater ground cover than the depauperate shrubs of the desert.

DISCUSSION

The nature of the physiognomic intergradation: continuum versus ecotone.—With respect to vegetation, the word continuum was used by Curtis and McIntosh (1951) to describe an ordination of species present in the broadleaf deciduous forest of Wisconsin. The species fell into a roughly linear sequence ranging from pioneer to climax. The use of these latter terms carries a strong implication that the Wisconsin continuum is, in part, an ordination of seral stages, but the door was not closed on a climax arrangement along an environmental gradient, or even a clisere. Hence, it seems that the word continuum

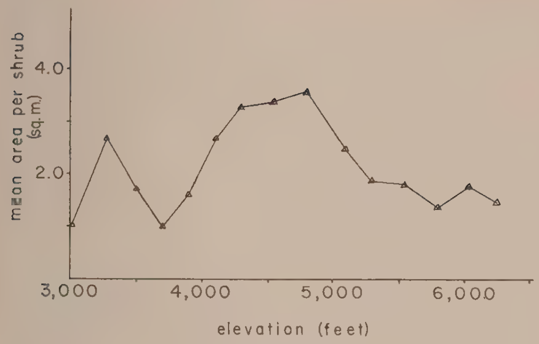

FIG. 2. Variation in mean area per shrub (the reciprocal of the absolute density) along the vegetational gradient correlated with elevation.

may be used in any of these senses. In the present discussion, *the word* continuum *will be used to mean climax communities overlapping continuously along an environmental gradient.*

The vegetation along the gradient in elevation is not sorted out into a series of tidy physiognomic zones separated by abrupt ecotones, but on the other hand it is far from being a physiognomic continuum. The vegetation of mixed physiognomy which exists between 4,000 and 5,000 ft is perhaps best interpreted as a matrix of shrubs on which a sparse coniferous woodland is superimposed "individualistically." This evergreen Pygmy Tree element never amounted to more than 15% of the individuals sampled at any one elevation, and played a minor role in this vegetation with respect to density. It is only from the standpoint of aspect dominance (*i.e.* conspicuousness) that pinyon and juniper assume importance here.

The shrub matrix in the elevation intervals between 3,000 and 3,250 ft, 4,100 and 4,300 ft and 5,800 and 6,000 ft provides the best evidence for a continuum or gradient in physiognomy. But such localized continua are little more than Clementsian ecotones at the zones of contact between physiognomically distinct formations. Furthermore, in the evergreen chaparral—deciduous woodland combination occurring at about 6,000 ft, the evergreen shrubs are distributed in dense clumps which form a mosaic with the open deciduous shrubs or small trees. Far from constituting an intimate and homogenous association, the two physiognomic types display considerable local incompatibility.

On the other hand, floristic gradients or continua were clearly evident within a given physiognomic type. For instance, there is a gradual decline in importance of *Quercus turbinella* in the evergreen chaparral, correlated with increasing elevation. It is replaced mainly by Garrya, Ceanothus, and Cercocarpus. Similarly, in the Pygmy Tree formation, *Juniperus osteosperma* carries the physiognomic type to desert elevations, while *Pinus monophylla* is the sole representative at the higher elevations. It is only at intermediate altitudes that the typical pinyon-juniper association is found, and the shift in relative importance of the two principal components with change in elevation is gradual.

Table I provides evidence for an overall floristic continuum in this vegetation, but Figure 1 shows that a true continuum in physiognomy is essentially lacking. Rather, the pattern of intergradation between widely different physiognomic types (the evergreen chaparral and the two contiguous deciduous formations) seems to hover between the continuous and the discontinuous. Indeed, the ecotones appear to be zones of competition between physiologically incompatible vegetation types.

Whittaker (1956) detected floristic gradients in the North American deciduous forest formation in the Great Smoky Mountains, and correlated them with ecological gradients. In essence, he showed that plant associations within the same formation intergrade rather continuously, because each component species has an individualistic distribution which does not usually coincide with those of its associates. However, he might have emphasized the lack of extensive gradation between two physiognomically divergent formations in the Smokies: the broadleaf deciduous forest and the evergreen spire forest of spruce and fir. There is such a narrow ecotone between these formations that one is tempted to call it not a transition but an "abruption," a word used by Transeau (1935) to describe the sharp boundary between deciduous forest and grassland of the prairie "peninsula" of the Middle West.

In general, there is evidence for extensive gradation of the continuum type between different associations of the same formation, but the ecotone between two physiognomically distinct formations usually occupies a relatively small fraction of their total areal extent. In other words, the width of the ecotone between two plant communities varies inversely with the differences in physiognomy and physiology which render them incompatible (environmental gradients being held equal). Interspecific competition, which is often neglected by excessively individualistic Gleasonians, is probably the key to an understanding of ecotones. Lack of competition (*e.g.* ecological isolation of two species on one microsite due to differential root stratification) is another side of the same coin.

Darwin (1859) sought an explanation for the lack of an abundance of transitional forms connecting systematic units in nature, because he felt that this constituted a weakness in his evolutionary theory. He suggested that competition would be keenest between organisms most closely related, and that very few of the proximal or intermediate forms would survive. This would eventually result in a series of disjunct types without close relatives. This concept may be applicable to the synthetic scale of ecological evolution, *i.e.* the selection of physiognomically distinct climax plant formations by particular mean climates, which have been stable in point of time, if not of space. One might also expect that, as in systematic evolution, the more successful dominant types would evolve in Darwin's "larger and more efficient workshops," where competition is most severe. With respect to ecological evolution, these would probably be located at the crossroads of genetic exchange in the central portion of a plant formation. Accordingly, the successful forms undergo a centrifugal dispersal until they meet competition from the dominants of contiguous formations, which have evolved under widely different mean climates. Thus, instead of a long graded series or continuum, one finds in nature a relatively small number of climax plant formations, of diverse physiognomy. These combine to form ecotones at zones of contact which are usually relatively small in area compared to the total area of each formation.

Variation in the zonation on different sides of the Pine Valley Mountains.—To recapitulate the transect on the southeastern side of the Pine Valley Mtns., the following vegetation zones may be defined as one progresses from 3,000 to 6,500 ft: Sonoran[3] Shrub (Larrea-Franseria), Mohavean[3] Shrub (Coleogyne), pinyon-juniper/Chaparral, Chaparral-Deciduous Woodland, *Pinus ponderosa* Forest. Sagebrush (*Artemisia tridentata*) is conspicuous by its absence as a vegetation zone on this side of the mountains, although abundantly present as a weed along trails, roadsides and in other disturbed areas. On the northwestern side of the mountains, however, the transition from warm desert to forest includes a broad sagebrush zone, while the chaparral and deciduous woodland zones are virtually absent. The zonation here is as follows: Sonoran Shrub, Mohavean Shrub, sagebrush, pinyon-juniper/sagebrush, pinyon-juniper, *Pinus ponderosa* Forest. The climatic difference between the two sides of the Pine Valley Mtns. probably accounts for the difference in vegetation: the southeastern side faces the warm, low-elevation Virgin River valley and is protected by the 10,000 foot range from the cold, winter air-masses which create the Great Basin climate on the northwestern side.

Influence of substratum on the zonation.—The Coleogyne zone has a peculiar extension of range to both higher and lower elevations on certain sedimentary rocks. On the southwest side of the mountain, Coleogyne forms a narrow ecotone with sagebrush at about 4,400 ft on alluvium and basalt, but reappears as a pure stand on outcrops of Jurassic limestone at over 5,000 ft. Here it is surrounded by sagebrush growing on alluvium. In the other direction, Coleogyne extends in pure stands down to 3,000 feet, or lower, on Triassic shale and sandstone outcrops; these are surrounded by Larrea on alluvium. The Larrea zone extends upward to about 3,500 feet on alluvium, where it forms an ecotonal combination with Coleogyne. Larrea and sagebrush are both evergreen, with a deep extensive rooting habit. They are probably favored with respect to the water factor by a deep, coarse, alluvial soil, especially here, near the limit of their ranges. Coleogyne, on the other hand, is deciduous and more shallowly rooted, and hence may be better adapted to the more ephemeral water supply in the thin residual soils of sedimentary rock outcrops.

[3] The low, arid intermountain basins, which comprise the greater part of the total area of the Mohave Desert, are dominated by Larrea and *Franseria dumosa*. It is only at higher elevations, on the less arid upper bajadas and mountain slopes, that the distinctive shrub flora of the Mohave Desert becomes evident. This characteristic assemblage of low, microphyllous, deciduous shrubs is appropriately termed the Mohavean Shrub zone. The evergreen Larrea zone may be termed the Sonoran Shrub zone, since it is an impoverished northward extension of the Sonoran Desert vegetation of Shreve (1951).

SUMMARY

The vegetation of the southeastern side of the Pine Valley Mountains was sampled along a gradient in elevation ranging from 3,000 to 6,000 ft. Beginning at the lower elevation, the following formations were found: Sonoran Shrub (Larrea-Franseria), Mohavean Shrub (Coleogyne), Pygmy Tree/Chaparral, Chaparral-Deciduous Woodland, Pine Forest (*Pinus ponderosa*).

Noteworthy is the presence in Utah of a true evergreen chaparral similar to that of central Arizona, which contains many of the dominant genera of the California chaparral. This chaparral largely usurps the zone usually occupied in southern Utah by pinyon-juniper/sagebrush vegetation. Another striking feature is the absence of shadscale and sagebrush zones. These are replaced here mainly by a deciduous shrub zone dominated by Coleogyne.

Floristic gradients of a continuous nature were present throughout the transect, but this does not enable one to recognize a continuum among the physiognomically distinct formations. It appears that the width of the ecotone between two plant communities varies inversely with the differences in physiognomy and physiology which render them incompatible.

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THE USE OF MULTIPLE REGRESSION AND CORRELATION IN BIOLOGICAL INVESTIGATIONS

INTRODUCTION

Many studies in ecology lend themselves to analysis by multiple regression and correlation. In many relationships, the actual contribution of each of any number of factors can be evaluated. Such evaluations can be made when several variates are suspected of affecting a result or in some way influencing the interpretation of results. For example, the results from various treatments in an experiment might be effectively evaluated by measuring one or two plant characteristics which are easily obtained, and from these data estimating still other plant responses which might be too time-consuming to measure otherwise. Stem height and plant density measurements have been used on annual grass types of California to estimate herbage production after various fertilizer treatments with satisfactory results (Evans and Jones 1958);

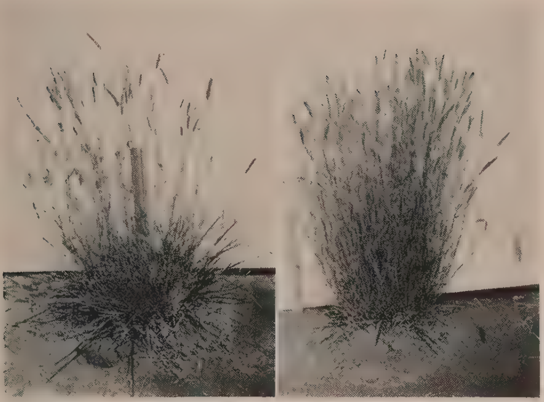

FIG. 1. Two plants of crested wheatgrass showing variability that may exist among plants. In the plant on the left, more herbage is produced near the base compared to the plant on the right.

and in Colorado, Wilm *et al.* (1944) used the product of height of plant times diameter to predict yield of bunchgrasses.

In another study Dewey and Lu (1959) used correlation and multiple regression to isolate the influence of seed size, spikelets per spike, and plant size upon seed yield. Shultz (1956) used multiple regression to show the relation of number of live stems, root crown diameter, length of current growth, and foliage crown cover to herbage production.

The author has measured the relation of soil moisture and exchangeable sodium in the soil to the number of plants of big sagebrush present on various sites in the Great Basin deserts; the effects of vigor measurements—such as leaf length, leaf widths, and length of current growth—upon forage yield of both desert shrubs and grasses; and the effects of basal area, height, and volume upon the yield of bunchgrasses. The latter has been chosen for presentation to illustrate the use of methods and techniques in carrying out such an analysis.

People often refer to volume of production as synonymous with weight of herbage produced. Volume technically refers to space occupied and is measured in cubic units. Actually, approximation of true volume of herbage can be accomplished by determining the average radius and height of a bunchgrass or a shrub. If these were measured in centimeters, then radius^2 x π x height would equal the cubic centimeters or liters of herbage.

Sometimes yield is estimated from height or basal area alone. However, a more appropriate index to yields can be obtained by measuring the basal area of the clump with a diameter rule which interprets the area directly from the diameter. This, multiplied by the average height, gives a volume index to herbage produced. Variability among plants is great; therefore, a combination of measures should be more reliable than a single one as an index to yield (Fig. 1).

PROCEDURE

In order to test the reliability of various plant measures as indexes of weight, 2150 clumps of crested wheatgrass were selected at random and measured for basal area and maximum height of the tallest seed culm. Every tenth plant was also harvested to determine dry weight. Calculations followed standard procedures for multiple regression and correlation presented by Goulden (1956), Ostle (1958), Snedecor (1956), and Cochran (1953).

Symbols

The following symbols and their interpretations are used in the analysis:

** = highly significant statistically: probability of chance occurrence less than 1 percent.

* = significant statistically: probability of chance occurrence less than 5 percent.

Y = the dependent variable or one of its values. Y is grams of dry weight.

X_1 = one independent variable or one of its values. X_1 is basal area in sq. cm.

X_2 = a second independent variable or one of its values. X_2 is height of the tallest culm in cm.

1 (or *2*) as a subscript is used for X_1 (or X_2).

$\bar{y}$ = the average of the Y's

$\bar{x}_1$ = the average of the X_1's

$\bar{x}_2$ = the average of the X_2's

$y = Y - \bar{y}$

$x_1 = X_1 - \bar{x}_1$

$x_2 = X_2 - x_2$

Y_e = value of Y expected or predicted from values of X_1 and/or X_2

S = sum of

$b_{Y1.2}$ = the (ordinary) partial coefficient of regression of Y on X_1 independent of X_2. This tells the *change* in Y (in grams) per *increase* of 1 sq. cm. in X_1 when X_2 is constant.

$b_{Y2.1}$ = the (ordinary) partial coefficient of regression of Y on X_2 independent of X_1. This tells the *change* in Y (in grams) per *increase* of 1 cm. in X_2 when X_1 is constant.

$b'_{Y1.2}$ = the *standard* partial coefficient of regression of Y on X_1 independent of X_2. This tells the number of standard deviations *change* in Y per *increase* of one standard deviation of X_1 when X_2 is constant.

$b'_{Y2.1}$ = the standard partial coefficient of regression of Y on X_2 independent of X_1. This tells the number of standard deviations *change* in Y per *increase* of one standard deviation of X_2 when X_1 is constant.

r_{Y1} = the coefficient of (simple) correlation of Y and X_1, when X_2 is not considered at all in the problem.

r_{Y2} = the coefficient of (simple) correlation of Y and X_2, when X_1 is not considered.

r_{12} = the coefficient of (simple) correlation of X_1 and X_2, when Y is not considered.

$(R_{Y.12})^2$ = the coefficient of multiple determination of Y by X_1 and X_2 when all three are considered in the problem. It tells the fraction of the (squared) variation of Y which is accounted for by both X_1 and X_2 (or is associated with X_1 and X_2).

$R_{Y.12}$ = the coefficient of multiple correlation of Y with X_1 and X_2 when all three are considered in the problem.

n = number of clumps or individuals.

$s_{Y.12}$ = the standard error of estimate when X_1 and X_2 are used. It is the standard deviation of the observed values from the predicted values, which are on the regression plane.

$s_{Y.1}$ = the standard error of estimate when only Y and X_1 are used. It is the standard deviation of the observed values from the predicted values.

$s_{Y.2}$ is similar to $s_{Y.1}$.

Data and calculations

For each grass clump in the subsample of 215 plants the Y (grams of dry weight), X_1 (the basal area), and X_2 (the height of the tallest seedhead) were determined. The calculations for the 215 individual plants are as follows:

$SY = 64{,}021$ g.
$\bar{y} = 297.77$ g.
$SX_1 = 39{,}275$ sq. cm.
$\bar{x}_1 = 182.67$ sq. cm.
$SX_2 = 19{,}146$ cm.
$\bar{x}_2 = 89.05$ cm.

The simplified formulas for calculating sum of squares and sum of products are:

$$Sy^2 = SY^2 - (SY)^2/n = 1{,}159{,}438 \tag{1}$$
$$Sx_1^2 = SX_1^2 - (SX_1)^2/n = 421{,}569 \tag{2}$$
$$Sx_2^2 = SX_2^2 - (SX_2)^2/n = 18{,}906 \tag{3}$$
$$Syx_1 = SYX_1 - (SY)(SX_1)/n = 303{,}183 \tag{4}$$
$$Syx_2 = SYX_2 - (SY)(SX_2)/n = 64{,}556 \tag{5}$$
$$Sx_1x_2 = SX_1X_2 - (SX_1)(SX_2)/n = 14{,}519 \tag{6}$$

The three simple correlation coefficients are computed in the following manner:

$$r_{Y1} = Syx_1/\sqrt{[(Sy^2)(Sx_1^2)]} = 303{,}183/\sqrt{[(1{,}159{,}438)(421{,}569)]} = \sqrt{(0.1881)} = 0.4337 \tag{7}$$

$$r_{Y2} = Syx_2/\sqrt{[(Sy^2)(Sx_2^2)]} = 64{,}556/\sqrt{[(1{,}159{,}438)(18{,}906)]} = \sqrt{(0.1901)} = 0.4360 \tag{8}$$

$$r_{12} = Sx_1x_2/\sqrt{[(Sx_1^2)(Sx_2^2)]} = 14{,}519/\sqrt{[(421{,}569)(18{,}906)]} = \sqrt{(0.02644)} = 0.1626 \tag{9}$$

The simple correlation coefficients are used to compute the standard partial regression coefficients:

$$b'_{Y1.2} = (r_{Y1} - r_{Y2}r_{12})/[1-(r_{12})^2] = [0.4337 - (0.4360)(0.1626)]/[1-0.02644] = 0.3727 \tag{10}$$
$$b'_{Y2.1} = (r_{Y2} - r_{Y1}r_{12})/[1-(r_{12})^2] = [0.4360 - (0.4337)(0.1626)]/[1-0.02644] = 0.3754 \tag{11}$$

The (ordinary) partial regression coefficients are required later to compute the multiple regression equation. Therefore the two (ordinary) partial regression coefficients are obtained as follows:

$$b_{Y1.2} = b'_{Y1.2}\sqrt{(Sy^2/Sx_1^2)} = (0.3727)\sqrt{[(1{,}159{,}438)/(421{,}569)]} = 0.6181 \text{ g./sq. cm.} \tag{12}$$

$$b_{Y2.1} = b'_{2.1}\sqrt{(Sy^2/Sx_2^2)} = (0.3754)\sqrt{[(1{,}159{,}438)/(18{,}906)]} = 2.9398 \text{ g./cm.} \tag{13}$$

Coefficients of determination

The multiple coefficient of determination $(R_{Y.12})^2$ which represents the total effect of both X_1 and X_2 upon yield is obtained from the following formula:

$$(R_{Y.12})^2 = b'_{Y1.2}r_{Y1} + b'_{Y2.1}r_{Y2} = (0.3727)(0.4337) + (0.3754)(0.4360) = 0.1616 + 0.1637 = 0.3253 \tag{14}$$
$$R_{Y.12} = \sqrt{(0.3253)} = 0.5704^{**} \tag{15}$$

To test whether $R_{Y.12}$ is statistically significant, refer to standard procedures presented in most statistic texts (Goulden 1956; Ostle 1958; Snedecor 1956). This is also a test of the significance of the entire multiple regression equation.

It is of interest to determine whether it was worthwhile to include both X_1 and X_2 variables in the regression-correlation analysis rather than one only. Therefore, the simple coefficient of determination when only X_1 is used is

$$(r_{Y1})^2 = (0.4337)^2 = 0.1881^{**} \tag{16}$$

and the simple coefficient of determination when only X_2 is used is

$$(r_{Y2})^2 = (0.4360)^2 = 0.1901^{**} \tag{17}$$

The multiple coefficient of determination was found to be

$$(R_{Y.12})^2 = 0.3253^{**}$$

The multiple coefficient of determination is considerably larger than either simple coefficient of determination. Therefore, it seems that it is desirable to include both X_1 and X_2 in predicting yield. The interpretation of the multiple coefficient of determination $(R_{Y.12})^2$ is that when both X_1 and X_2 are used together they account for 32.53% (0.3253) of the variation in Y.

From equation 14 we see that when both X_1 and X_2 are included, X_1 accounts for 16.16% (0.1616) of the variation in Y, and X_2 accounts for 16.37% (0.1637) of the variation in Y. When only X_1 is included in the computation, it accounts for 18.81% (0.1881) (equation 16) of the variation in Y. This is larger than 0.1616, the variation accounted for by X_1 when both X_1 and X_2 are included. Variables X_1 and X_2 are correlated ($r_{12} = 0.1626$) (equation 9). Therefore, even if only X_1 is used in the computation, X_2 has an effect because of its correlation with X_1. This is the reason that when only X_1 is included it accounts for more of the variation in Y (0.1881) than it accounts for when both X_1 and X_2 are included (0.1616). For the same reason, when only X_2 is used it accounts for more of the variation in Y (0.1901) (equation 17) than it accounts for when both X_1 and X_2 are included (0.1637). Also for the same reason

$$(r_{Y1})^2 + (r_{Y2})^2 = 0.1881 + 0.1901 = 0.3782 \tag{18}$$

is greater than

$$(R_{Y.12})^2 = 0.3253.$$

In $(R_{Y.12})^2$ the effect of each X has been included only once, whereas in $(r_{Y1})^2 + (r_{Y2})^2$ part of the effect of each X has been included twice.

Testing significance of partial regression coefficients

Tests of significance of the individual partial regression coefficients may be desired to evaluate the reliability of the relation of the independent variables to the dependent variable.

If only tests of significance of the partial regression coefficients are desired, the easiest method is to test the b-primes because both have the same standard error.

The standard error for either $b' = s_b'$

$$= \sqrt{[(1-(R_{Y.12})^2)/(1-(r_{12})^2)(n\text{-}3)]} = \sqrt{[(1-0.3253)/(1-0.02644)(215-3)]} = \sqrt{[0.003269]} = 0.05718 \tag{19}$$

For the test of significance for $b'_{Y1.2}$

$$t = b'_{Y1.2}/s_b' = 0.3727/0.05718 = 6.53^{**} \tag{20}$$

For the test of significance for $b'_{Y2.1}$

$$t = b'_{Y2.1}/s_b' = 0.3754/0.05718 = 6.57^{**} \tag{21}$$

Both b-primes are highly significant, with less than 1 percent probability because both *t's* are larger than the 1 percent *t* value (2.58).

If confidence intervals for the *b* values as well as tests of significance of the partial regression coefficients are wanted, there is no object in testing the b-primes. Instead proceed as follows:

Compute a divisor, *D*, as a first step in the use of Gauss multipliers:

$$D = (Sx_1^2)(Sx_2^2) - (Sx_1x_2)^2 = (421{,}569)(18{,}906) - (14{,}519)^2 = 7{,}759{,}382{,}153 \qquad (22)$$

Then compute the Gauss multipliers c_{11}, c_{22}, and c_{12}. These are sometimes referred to as elements of the inverse matrix.

$$c_{11} = Sx_2^2/D = 18{,}906/7{,}759{,}382{,}153 = 0.000{,}002{,}437 \qquad (23)$$

$$c_{22} = Sx_1^2/D = 421{,}569/7{,}759{,}382{,}153 = 0.000{,}054{,}330 \qquad (24)$$

$$c_{12} = Sx_1x_2/D = -14{,}519/7{,}759{,}382{,}153 = -0.000{,}001{,}871 \qquad (25)$$

The standard error of each partial regression coefficient is computed as follows:

$$sb_{Y1.2} = \sqrt{[c_{11}(s_{Y.12})^2]} = \sqrt{[(0.000{,}002{,}437)(3{,}689.97)]} = \sqrt{(0.00897)} = 0.0947 \qquad (26)$$

$$sb_{Y2.1} = \sqrt{[c_{22}(s_{Y.12})^2]} = \sqrt{[0.000{,}054{,}330)(3{,}689.97)]} = \sqrt{(0.1999)} = 0.4471 \qquad (27)$$

For the test of $b_{Y1.2}$

$$t = b_{Y1.2}/sb_{Y1.2} = 0.6181/0.0947 = 6.53^{**} \qquad (28)$$

For the test of $b_{Y2.1}$

$$t = b_{Y2.1}/sb_{Y2.1} = 2.9398/0.4471 = 6.57^{**} \qquad (29)$$

As they should be, these *t* values for testing the *b's* are the same as the *t* values for testing the b-primes.

The b-primes (standard partial coefficients) have only two advantages over the *b's* (ordinary partial coefficients). The relative importance of X_1 and X_2 in relation to *Y* is shown by the b-primes as well as by the $(r_{Yi})^2$ but not by the *b's*. The $b'_{1.2}$ (=0.3727) is less than $b'_{Y2.1}$ (= 0.3754); therefore, X_1 variable is slightly less important than X_2 in relation to *Y*. It is a coincidence that the two b-primes are so nearly equal in this case. In this problem both b' and b for X_2 are larger than for X_1, but in other cases the order of size of the *b*-primes and the *b's* may be reversed, depending upon the units of measure and their magnitudes. The second advantage of the *b*-primes is that they can be tested for significance by one standard error, whereas each *b* requires its own standard error. However, the *b*-primes lose this advantage if confidence intervals are desired for the *b's* and/or for predicted values of *Y*.

Volume as a third variate

A third variable representing liters of volume in a clump of grass can be calculated from X_1 (sq. cm. of basal area) and X_2 (height in centimeters). The third variable X_3 (liters) $= (X_1)(X_2)/1000$.

Data calculated for X_3 variable for the subsample of 215 plants is as follows:

$$SX_3 = 3{,}547.5$$

$$\bar{x}_3 = 16.50$$

$$Sx_3^2 = SX_3^2 - (SX_3)^2/n = 4{,}297 \qquad (30)$$

$$Syx_3 = SYX_3 - (SY)(SX_3)/n = 35{,}966 \qquad (31)$$

The simple correlation coefficient for X_3 and *Y* is

$$r_{Y3} = Syx_3/\sqrt{(Sy^2)(Sx_3^2)} = 0.5095 \qquad (32)$$

and the simple coefficient of determination when only *Y* and X_3 are used is

$$(r_{Y3})^2 = 0.2596$$

The variable X_3 (volume) alone accounts for 25.96 percent of the variation in *Y*. Thus, volume (X_3) is by far the best of the three single determinations for accounting for variation in *Y*.

The use of regression and correlation in double sampling

In many studies dealing with plant responses it is desirable to measure herbage production as a major response to treatment. Measuring production by harvesting plots is time consuming and as a result is much too costly when many samples are required. For this reason the method of double sampling is sometimes used. In this method only a relatively small number of samples are actually harvested, but by measuring specific plant characteristics associated with yield, on a larger sample, the predicted yield can be obtained from a simple regression or multiple regression equation. The regression equation to be used is derived from the samples that are harvested and otherwise measured for indexes for predicting yield.

In order to compare some of the results from multiple regression-correlation using partial regression coefficients with results from simple regression-correlation using only simple regression coefficients, further computations follow.

The first calculations concern the use of *Y* and X_1 without consideration for X_2. It may be assumed that X_2 and X_3 were not measured.

The coefficient of regression of *Y* on X_1 is

$$b_{Y1} = Syx_1/Sx_1^2 = 303{,}183/421{,}569 = 0.7192 \text{ g./sq. cm.} \qquad (33)$$

A similar computation with *Y* and X_2 without consideration for X_1 and X_3 is

$$b_{Y2} = 64{,}556/18{,}906 = 3.4146 \text{ g./cm.} \qquad (34)$$

and for *Y* and X_3 without X_1 and X_2 is

$$b_{Y3} = Syx_3/Sx_3^2 = 35{,}966/4{,}297 = 8.370 \text{ g/liter} \qquad (35)$$

All of the plants were measured for the independent variables X_1, X_2, and X_3 but only 10 percent were harvested to obtain the values for yield (*Y*). The large sample of size 2,150 (n') and the partial sample of size 215 (n) are used first to estimate the average yield (y') for the large sample of 2,150 plants. The mean values from the large sample are $\bar{x}'_1 = 185.33$, $\bar{x}'_2 = 89.17$, and $\bar{x}'_3 = 16.84$. The estimated average yield from $\bar{x}'_1$ can be obtained from the following simple regression equation:

$$\bar{y}' = \bar{y} + b_{Y1}(\bar{x}'_1 - \bar{x}_1).$$

$$\bar{y}'_1 = 297.77 + 0.7192\,(185.33 - 182.67) = 300.00 \qquad (36)$$

The variance for the estimated average yield ($v'\bar{y}_1$) from X'_1 for the large sample can be found by

$$v'\bar{y}_1 \quad \frac{Sy^2(1 - r_{y1}^2)}{n}\left(1 + \frac{n'-n}{n'}\,\frac{1}{(n-3)} + \frac{r_{Y1}^2\,Sy^2}{n'}\right)$$

$$v'\bar{y}_1 \quad \frac{1{,}159{,}438\,(1 - 0.1881)}{215}\left(1 + \frac{2{,}150 - 215}{2{,}150}\,\frac{1}{215 - 3}\right) + \frac{(0.1881)(1{,}159{,}438)}{2{,}150} = 4{,}498.36 \qquad (37)$$

The 95 percent confidence interval for estimated average yield from $\bar{x}_1$ can be found by

$$\bar{y}'_1 \pm t_{.05}\sqrt{v'\bar{y}_1}$$

$$300.00 \pm (1.96)\sqrt{4{,}498.36} = 300.00 \pm 131.46 \qquad (38)$$

TABLE 1. Average estimated yield ($\bar{y}'$) from measurements of independent variables X'_1, X'_2, and X'_3 on 2,150 random sampled plants from regression equations calculated from a subsample of 215 plants, and confidence intervals calculated from each independent variable by simple regression compared to calculations from multiple regression with X'_1 and X'_2.

Regression variables	Estimated average yield ($\bar{y}'_i$)	Confidence interval.[1] ($t_{.05}$)($s'_{\bar{y}i}$)
Simple from $\bar{x}'_1$	300.00	131.46
Simple from $\bar{x}'_2$	298.12	131.30
Multiple from $\bar{x}'_1$ and $\bar{x}'_2$	299.76	121.28
Simple from $\bar{x}'_3$	297.77	126.26

[1] Add this value to the mean and likewise subtract it from the mean to obtain the confidence interval.

Similar calculations were made for X'_2 and X'_3 and are shown in Table I.

The average variance calculated by the above formula assumes that the large sample (n') is drawn at random, and the small or partial sample (n) is a random subsample of the larger sample.

The estimated mean yield from both $\bar{x}'_1$ and $\bar{x}'_2$ is obtained by the following multiple regression equation:

$$\bar{y}'_{12} = \bar{y} + b_{Y1.2}(\bar{x}'_1 - \bar{x}_1) + b_{Y2.1}(\bar{x}'_2 - x_2) = 297.77 + 0.6181\ (185.33 - 182.67) + 2.9398\ (89.17 - 89.05) = 299.76 \tag{39}$$

The average variance for the estimated mean from both X'_1 and X'_2 follows

$$v'\bar{y}_{12} = \frac{Sy^2\,(1 - R^2_{Y12})}{n}\left(1 + \frac{n' - n}{n'}\ \frac{1}{(n-3)}\right) + \frac{R^2_{Y12}\,Sy^2}{n'} = \frac{1{,}159{,}438\ (1 - 0.3253)}{215}\left(1 + \frac{2{,}150 - 215}{2{,}150}\ \frac{1}{215 - 3}\right) + \frac{(0.3253)\ (1{,}159{,}438)}{2{,}150} = 3{,}829.34 \tag{40}$$

The 95 percent confidence interval estimated yield from $\bar{x}'_1$ and $\bar{x}'_2$ is

$$\bar{y}'_{12} + t_{.05}\sqrt{v'\bar{y}_{12}}$$

$$299.76 \pm (1.96)\sqrt{3{,}829.34} = 299.76 \pm 121.28 \tag{41}$$

The estimated average yield ($\bar{y}'$) from the three simple regression equations and the multiple regression equation were, as would be expected, all about the same (Table I). However, the confidence intervals are smaller for those variables or combination of variables accounting for the greater variation in yield (Y). Therefore the use of basal area and height in a multiple regression equation is the best of the three for predicting yield, and volume is next.

The variation unaccounted for by the variables is a result of varying density of the herbage in the clump and the uniformity of growth of all culms with respect to the tallest culm measured. Refinement in measuring variables of a grass clump to account for more of the variation in yield of herbage should consider indexes to density within the clump along with volume. In addition, the average of culm height should be determined rather than height of tallest seed culm in the clump. Any improvement in measurements or additional measurements leading to greater variation in Y accounted for will reduce the size of the confidence interval and result in greater precision in estimating yield.

If rather small differences in treatment yields are to be evaluated from predicted values, the investigator must seek measurable characteristics that will account for a high percentage of the variability in yield. As can be noted in equations 37 and 40, a great many subsamples are required to compensate for large percentages of unaccounted for variation in Y as shown by $(1 - r_{Y1}{}^2)$ and $(1 - R^2_{Y12})$.

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A PHOTOTUBE SOLAR RADIATION INTEGRATOR FOR ENVIRONMENTAL STUDIES[1]

INTRODUCTION

The measurement of differences in light climate between and within vegetation types has long been difficult. The convenience of exposure meters or photometers in microclimatic studies is offset by the difficulties involved in adequate sampling and reduction of the data obtained. Instruments capable of integrating incident light energy are usually bulky and expensive, which limits their usefulness in field studies. Recording photoelectric integrators are described by Middleton (1953), Ogden (1954), Somers and Hamner (1951), and Sprague and Williams (1943). Despite these recent advances in the measurement of light climate, there is a need for an inexpensive, portable, field survey integrator. The device described in this paper is essentially a modification of the circuit described by Poole (1928), who placed a small capacitor in series with a vacuum phototube and a battery. A small neon glow lamp in parallel with the capacitor flashed when the voltage across the capacitor exceeded the ionization potential of the glow lamp. The instrument described here has been modified to produce an audible signal as well as a visual signal, and the photoreceptor has been modified to provide spherical illumination (Middleton 1943, Shirley 1945). The response of the instrument is linear with increments of radiation. A range-changing device increases the sensitivity of the integrators to light of low intensities. The instrument can be assembled from parts available at an electronic supply house for approximately $20.

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[1] Contribution from the Botanical Laboratory of the University of Tennessee, n. s. No. 204.

Components

The general construction of the integrator is shown in Figure 1. The instrument case is made of aluminum and measures 3 in. by 4 in. by 5 in. The earphones are connected to a phone jack on the instrument case. The photoreceptor is made of heat-formed opalescent lucite and is mounted in an automobile tail-light retaining ring.

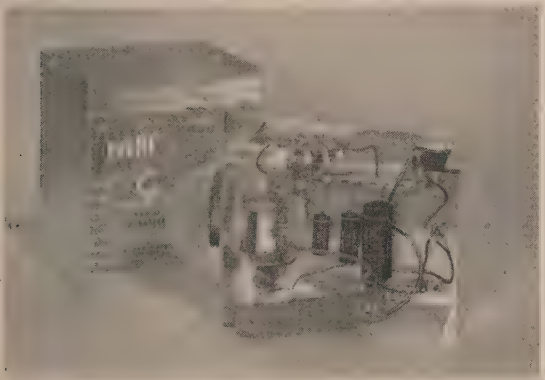

Fig. 1. Internal view of integrator showing battery, photocell, capacitors, range-changing switch, on-off switch, phone jack, neon glow lamp (below photocell), and photoreceptor.

The phototube must be screened to receive less than 500 ft-c under conditions of maximum illumination. A filter designed for this purpose is inserted at the base of the photoreceptor. Substitution of a filter carrier makes possible the use of narrow band Wratten filters for studies of the qualitative composition of incident radiation. Light reduction is achieved by a perforated aluminum foil disc sandwiched between two opal glass plates. The number of perforations is determined empirically. It is possible to increase the sensitivity of the instrument approximately 20 times by removing the opal glass plate reduction filter. At very low levels of illumination (0.1-1.0 ft-c), the internal capacitance of the integrator, as well as "dark current" caused by electron drift across the phototube may decrease the accuracy of measurement.

The phototube which is most suitable for field use is the RCA 926 (S3 photo-response, output 0.0016 μa/μw at 420 mμ). The relative sensitivity curve for the RCA 926 phototube is compared with the Weston Photronic Cell (Viscor filter) in Figure 2. The response of the RCA 926 (max. at 425 mμ) more closely approximates the absorption spectrum of chlorophyll (max. at 430 mμ and 660mμ) than the Weston Photronic cell (max. at 550 mμ). Although neither photocell is uniformly sensitive to different wave lengths of light, the RCA 926 represents a closer approximation to the biologically active portions of the spectrum than the selenium barrier-layer photocell of conventional photometers.

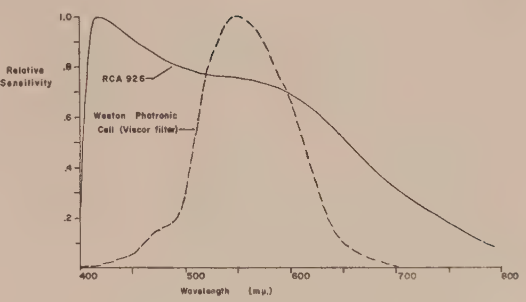

Fig. 2. Relative sensitivity of RCA 926 vacuum phototube compared with Weston Photronic Cell (with Viscor filter). Values are expressed as a per cent of maximum response.

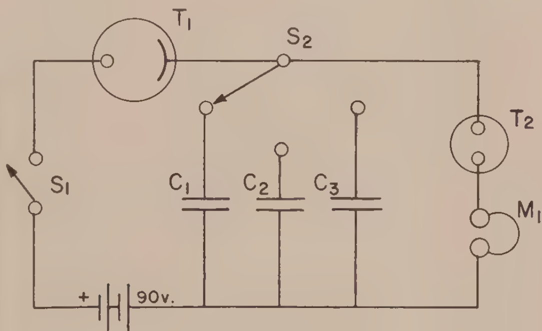

Fig. 3. Circuit diagram for integrator. T_1 = photocell; T_2 = NE-51 glow lamp; M_1 = earphones; S_1 = on-off switch; S_2 = SP3T switch; C_1, C_2, C_3 = capacitors. Battery is 90v radio "B" battery.

The operating potential of the RCA 926 is 90v, which can be maintained by a radio "B" battery such as the Burgess N60 or the RCA VS090. There is very little current drain by the circuit and satisfactory operation can be expected for the shelf life of the batteries (one instrument has been operating dependably on the same battery for 15 months).

A range-changing switch permits the use of different capacitances in the circuit. The glow lamp is an NE-51 and may be mounted in a Drake 50 pilot light assembly to provide a visual signal, or inside the instrument if only an auditory signal is desired.

Circuit Operation

The circuit (Figure 3) includes the phototube (T_1), glow lamp (T_2), earphones (M_1), range-changing switch (S_2), capacitors (C_1, C_2, and C_3), on-off switch (S_1), and battery. In operation light striking the phototube (T_1) generates a small current which is accumulated on the capacitor. When the ionization potential of the glow lamp (T_2) is reached, a discharge takes place, producing an audible click in the earphones. The number of clicks in a unit of time is a measure of the amount of radiation falling on the phototube during that time. The values of the 3 capacitors have been chosen to pro-

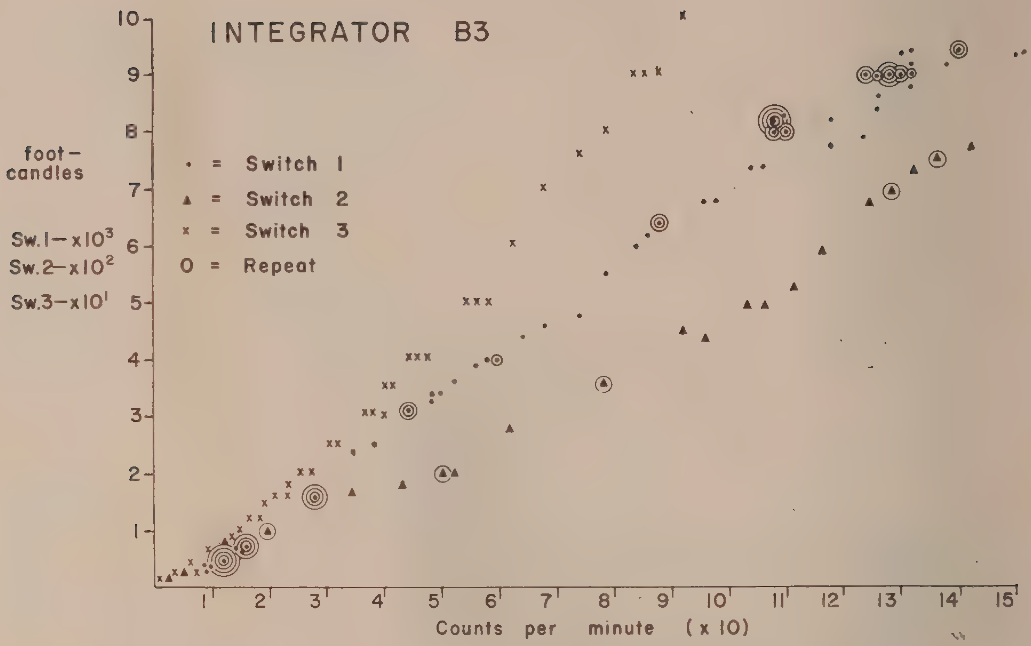

FIG. 4. Calibration data for Integrator B_3. Circled points indicate duplicate observations.

vide decade response to levels of illumination. The C_1 capacitor (0.1 μf) discharges approximately 100 times per minute at 10,000 ft-c. The C_2 capacitor (0.01 μf) discharges approximately 100 times per minute at 1000 ft-c. The C_3 capacitor (0.001 μf) discharges approximately 100 times per minute at 100 ft-c. The values of capacitors will vary (± 10%), and each set should be calibrated to insure proper sensitivity.

CALIBRATION

The integrators may be calibrated with any light-measuring instrument of recognized precision. Calibration data for Integrator B3 (Figure 4) are the result of a series of observations over 3 months.

The tendency toward logarithmic response in switch positions 2 and 3 is a result of the internal capacitance of the instrument and is constant for each integrator. The calibrations are stable as long as the circuit components are unchanged. The phototubes will eventually lose sensitivity after prolonged exposure to high intensity radiation. Fatigue tests performed for 3 months on Integrator B3 showed no appreciable change in values, however. the tests were performed by operating the instrument continuously during daylight hours for 3 months.

It is suggested that a calibration check be performed at least once a season, or as often as the battery is changed.

CONCLUSION

A principal disadvantage of phototube solar radiation integrators is the fact that they are not uniformly sensitive to different wave-lengths of light. Although they may be calibrated in absolute energy units, changes in the spectral composition of incident radiation will affect the calibration values. The same objections, however, hold for existing radiation-measuring devices. Phototube solar radiation integrators have several features which make them attractive as ecological research tools. Their portability, low initial expense and maintenance, and their property of recording total incident radiation invite their use in climatological investigations of plant environments.

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THE pH OF FRESH SOILS AND SOIL SOLUTIONS[1]

Development of robust glass electrodes in recent years has made possible direct reading of pH on the fresh material of many soils, especially in the rather organic surface horizons characteristic of moist temperate climates, and in aquatic soils. It is well known that such readings, which involve packing moist soil around the electrodes, are often a good deal lower than those made on soil solutions, which may themselves exhibit a marked rise in pH upon stirring and expulsion of excess carbon dioxide. However, the magnitude of the differences has seldom been examined in natural soils, and is sometimes not appreciated by ecologists and others making pH measurements on them.

This communication reports the range of pH values obtained for a series of British soils. Table I presents data from (a) highly organic *mor* humus layers in oakwoods, (b) much less organic *mull* humus layers in mixed hardwoods, and (c) a 4-meter mud core from the deepest part of a fertile lake, Esthwaite Water. All samples were collected in the English Lake District, and the woodland soils have been described previously (Gorham 1953, 1958 a).

It is evident that the lowest pH values were obtained by direct insertion of the electrodes into fresh soil, which exposed them to contact with swarms of absorbed cations concentrated at the surfaces of soil colloids (the so-called "suspension effect" (Jenny *et al.* 1950). The individual pH readings in this case were 0-1.3 units below those made on fresh soil solutions immediately after expression by a hydraulic press, the differences averaging 1.0 unit in the *mulls,* 0.9 unit in the *mors,* and only 0.4 unit in the much wetter aquatic soils, which did not require so much packing around the electrodes. The freshly collected soil solutions in turn gave readings of 0-1.8 pH units below those obtained after aeration, which reduced carbon dioxide tension to the level of atmospheric equilibration. In this instance the greatest rise on aeration (average 1.3 units) was exhibited by the lake muds, where escape of respired carbon dioxide to the atmosphere is greatly impeded. The average increase in the *mulls* amounted to 0.7 unit, while in the strongly acid *mors* it was negligible.

The extremely low pH values of the expressed *mor* solutions were due to the presence of free sulfuric acid (Gorham 1958 b), while the faint acidity of the fresh solutions from *mulls* and lake muds was obviously due mainly to dissolved carbon dioxide, since the values rose markedly upon aeration, to above the neutral point except in two of the *mulls.* The alkaline pH values in the mud solutions after aeration, and in three of the *mull* solutions, were no doubt due to the presence of bicarbonates, calcium bicarbonate being the chief product of soil weathering in this area (Gorham 1958 a).

TABLE I. Three methods of pH measurement on natural soils of the English Lake District

	pH BY GLASS ELECTRODE		
	Direct insertion	Expressed solution	Aerated solution
Mor humus layers	3.5	3.9	3.9
	3.4	4.1	4.1
	3.4	4.3	4.3
	3.5	4.5	4.5
	3.3	4.6	4.8
Mull humus layers	4.6	5.9	6.5
	5.3	6.0	6.6
	5.4	6.2	7.1
	5.7	6.5	7.3
	5.4	6.6	7.1
Lake muds*			
depth in core (cm.)			
20- 40	6.5	6.8	8.1
80-100	6.4	6.8	8.5
100-120	6.3	6.6	8.4
160-180	6.3	6.8	8.0
220-240	6.2	6.7	8.0
250-270	6.2	6.8	8.3
290-310	6.3	7.0	8.4
340-360	6.3	6.8	8.2
385-405**	6.6	6.6	7.1

* pH of water above mud 6.8, rising to 7.6 after aeration.
** Mud less organic and somewhat clayey.

In conclusion it may be remarked that the maximum difference, between pH by direct electrode insertion and by measurement on expressed and aerated soil solutions, may reach 1.5 units in the *mors,* 1.9 units in the *mulls,* and 2.1 units in the lake muds; averaging 0.9, 1.6 and 1.8 units respectively.

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[1] This work was done while the author was on the staff of the Freshwater Biological Association, Ambleside, England.

NOTE ON THE DISTRIBUTION OF PANDALIDAE (CRUSTACEA, DECAPODA) IN NEW ENGLAND WATERS

Introduction

Four species of the family Pandalidae are common bottom-dwelling inhabitants of the offshore waters of New England; they are: *Dichelopandalus leptocerus* (Smith), *Pandalus borealis* Kröyer, *Pandalus montagui* Leach, and *Pandalus propinquus G. O. Sars.* Three additional species—*Plesionika tenuipes* (Smith), *Plesionika acanthonotus* (Smith), and *Heterocarpus carinatus* (Smith)—occur in New England waters, but because of their relative scarcity in the area sampled they will not be considered further in this report.

The 4 common species are rather large shrimps, the largest that occur in sublittoral waters of this region. Adults of all 4 species attain body lengths of 2 to 5 inches or more. The larger specimens are of a size presently acceptable for consumption in North America, although they are somewhat smaller than the Penaeidae—the shrimps commonly marketed in the United States and Canada. *Pandalus borealis,* the largest New England pandalid shrimp, supported a small commercial fishery in Maine and Massachusetts from 1933 to 1950 (Scattergood 1952). The fishing grounds for these stocks were limited to small coastal areas in the western Gulf of Maine, but as the abundance of shrimp diminished the fishery gradually terminated. However, assuming a continued market demand for shrimp, it may be anticipated that slightly smaller species may be sought in the future. Thus, there is a continued interest in the distribution and abundance of all New England pandalid shrimps.

A study of the more significant literature (Smith and Harger 1874; Smith 1879, 1881, 1882, 1884, 1887; R. Rathbun 1883; M. J. Rathbun 1905, 1929; Walford 1936;

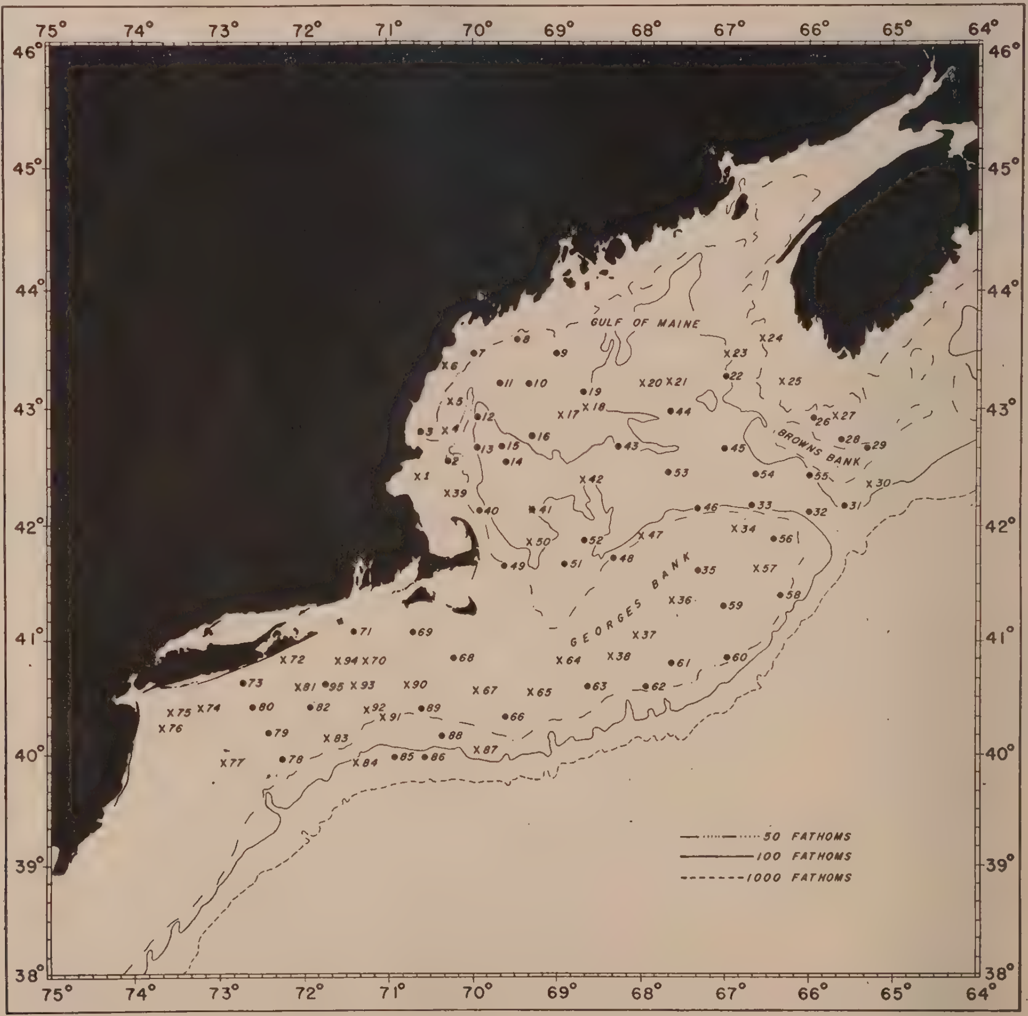

FIG. 1. Chart of New England region with trawling stations plotted. Stations where pandalid shrimp were caught are indicated by solid circles (●); stations where none were caught are indicated by crosses (x).

TABLE I. Station data and catch records of shrimp for *Albatross III* cruises 81 and 82, November 1956

Station	Date	Time (E. S. T.)	Latitude (north)	Longitude (west)	Water depth (fathoms)	Bottom water temperature (°F.)	NUMBER CAPTURED			
							Dichelopandalus leptocerus	Pandalus borealis	Pandalus montagui	Pandalus propinquus
1	2	1140	42°24′	70°40′	36	49.5	—	—	—	—
2	2	1525	42°33′	70°20′	62	46.0	4	1	—	—
3	2	1838	42°48′	70°36′	46	44.7	7	—	1	—
4	2	2145	42°49′	70°22′	75	42.6	—	—	—	—
5	3	0055	43°04′	70°18′	59	43.6	—	—	—	—
6	3	0350	43°20′	70°19′	24	49.0	—	—	—	—
7	3	0745	43°28′	69°58′	66	—	84	—	15	—
8	3	1110	43°38′	69°20′	70	—	1	—	—	—
9	3	1422	43°30′	68°59′	70	48.2	12	—	—	—
10	3	1713	43°14′	69°15′	90	42.8	—	1	—	12
11	3	2005	43°14′	69°36′	74	44.7	20	1	—	3
12	3	2220	42°58′	69°56′	106	—	—	2	—	—
13	4	0150	42°43′	69°56′	98	42.7	1	1	—	2
14	4	0500	42°33′	69°38′	143	44.9	2	—	—	3
15	4	0740	42°48′	69°39′	100	—	17	3	—	13
16	4	1024	42°50′	69°18′	42	43.2	45	—	—	—
17	4	1345	42°57′	68°58′	50	—	—	—	—	—
18	4	1715	42°58′	68°40′	102	45.0	—	—	—	—
19	4	1940	43°12′	68°38′	86	40.1	—	2	—	—
20	5	0010	43°13′	68°00′	124	—	—	—	—	—
21	5	0345	43°13′	67°39′	136	—	—	—	—	—
22	5	0820	43°14′	66°58′	102	—	—	—	1	58
23	5	1115	43°29′	66°58′	105	—	—	—	—	—
24	5	1423	43°36′	66°35′	56	54.0	—	—	—	—
25	5	1726	43°16′	66°19′	36	52.0	—	—	—	—
26	5	2125	42°58′	65°57′	70	47.1	—	—	4	—
27	6	0025	42°59′	65°40′	72	41.0	—	—	—	—
28	6	0250	42°42′	65°40′	50	49.5	1	—	64	—
29	6	0610	42°42′	65°18′	50	46.0	1	—	8	—
30	6	0822	42°24′	65°14′	62	40.0	—	—	—	—
31	6	1152	42°11′	65°35′	94	43.6	1	—	—	—
32	6	1430	42°10′	65°57′	124	—	19	—	3	3
33	6	1925	42°10′	66°35′	73	43.5	74	—	6	—
34	6	2215	41°54′	66°55′	33	52.7	—	—	—	—
35	7	0125	41°40′	67°16′	27	55.5	1	—	—	—
36	7	0545	41°22′	67°35′	19	55.2	—	—	—	—
37	7	0900	41°06′	67°56′	20	54.6	—	—	—	—
38	7	1100	40°50′	68°18′	20	55.6	—	—	—	—
39	8	1000	42°16′	70°18′	12	50.7	—	—	—	—
40	8	1215	42°10′	69°57′	78	42.0	11	2	—	—
41	8	1615	42°10′	69°22′	106	42.9	—	—	—	—
42	8	1915	42°25′	68°40′	108	43.0	—	—	—	—
43	8	2338	42°42′	68°19′	97	44.2	2	—	—	31
44	9	0400	42°54′	67°47′	97	43.8	5	—	—	34
45	9	0930	42°42′	66°58′	119	47.1	7	—	—	—
46	10	1315	42°09′	67°16′	79	44.0	28	—	—	—
47	10	1740	41°56′	67°55′	36	49.1	—	—	—	—
48	10	2045	41°44′	68°15′	30	—	90	—	—	1
49	13	2317	41°38′	69°38′	38	50.3	38	—	10	—
50	14	0220	41°54′	69°17′	107	42.2	—	—	—	—
51	14	0550	41°40′	68°58′	74	41.1	52	—	—	—
52	14	0830	41°53′	68°39′	93	41.6	7	—	—	—
53	14	1500	42°25′	67°38′	126	46.0	—	—	—	40
54	14	2030	42°28′	66°42′	180	46.0	30	—	—	56
55	15	0105	42°27′	66°00′	108	48.0	1	—	—	—
56	15	0600	41°54′	66°16′	47	52.3	1	—	—	—
57	15	0920	41°40′	66°36′	36	52.8	—	—	—	—
58	15	1230	41°28′	66°24′	51	52.3	1	—	—	—
59	15	1615	41°22′	66°57′	35	52.7	14	—	—	—
60	15	2028	40°52′	66°56′	50	60.7	24	—	—	—
61	16	0045	40°50′	67°36′	40	56.0	28	—	—	—
62	16	0405	40°36′	67°56′	48	63.0	61	—	—	—
63	16	0820	40°35′	68°36′	35	67.7	1	—	—	—
64	16	1125	40°50′	68°56′	37	61.8	—	—	—	—
65	16	1423	40°36′	69°16′	28	54.7	—	—	—	—
66	16	1840	40°20′	69°38′	38	63.5	14	—	—	—
67	16	2115	40°34′	69°58′	32	63.0	—	—	—	—
68	17	0030	40°50′	70°13′	20	53.0	17	—	—	—
69	17	0340	41°04′	70°45′	25	58.3	139	—	—	—
70	17	0727	40°51′	71°14′	32	—	—	—	—	—

TABLE I. (Continued)

Station	Date	Time (E. S. T.)	Latitude (north)	Longitude (west)	Water depth (fathoms)	Bottom water temperature (°F.)	Number Captured: Dichelopandalus leptocerus	Pandalus borealis	Pandalus montagui	Pandalus propinquus
71	17	1010	41°04′	71°24′	23	61.5	1	—	—	—
72	17	1445	40°52′	72°12′	16	59.0	—	—	—	—
73	17	1751	40°38′	72°44′	18	55.8	69	—	—	—
74	17	2117	40°23′	73°13′	18	56.6	—	—	—	—
75	17	2338	40°23′	73°34′	11	56.8	—	—	—	—
76	18	0200	40°14′	73°41′	18	—	—	—	—	—
77	18	1610	39°58′	72°58′	26	—	—	—	—	—
78	18	2040	39°56′	72°18′	38	58.0	5	—	—	—
79	18	2315	40°09′	72°25′	32	58.0	11	—	—	—
80	19	0138	40°22′	72°36′	26	56.0	29	—	—	—
81	19	0530	40°36′	72°06′	26	57.6	—	—	—	—
82	19	0720	40°26′	71°57′	36	61.0	1	—	—	—
83	19	1000	40°11′	71°46′	43	59.0	—	—	—	—
84	19	1235	39°58′	71°38′	59	56.8	—	—	—	—
85	19	1430	40°00′	70°54′	184	—	4	—	—	—
86	19	1850	39°58′	70°38′	186	—	7	—	—	—
87	19	2248	40°02′	70°00′	78	—	—	—	—	—
88	20	0210	40°06′	70°10′	64	57.6	2	—	—	—
89	20	0420	40°23′	70°34′	46	59.0	36	—	—	—
90	20	0655	40°38′	70°44′	34	61.0	—	—	—	—
91	20	1050	40°20′	71°04′	77	56.7	—	—	—	—
92	20	1315	40°22′	71°13′	43	62.0	—	—	—	—
93	20	1540	40°36′	71°23′	34	60.5	—	—	—	—
94	20	1610	40°50′	71°36′	32	62.0	—	—	—	—
95	20	2030	40°39′	71°44′	33	62.5	86	—	—	—
						Total number	1,112	13	112	256

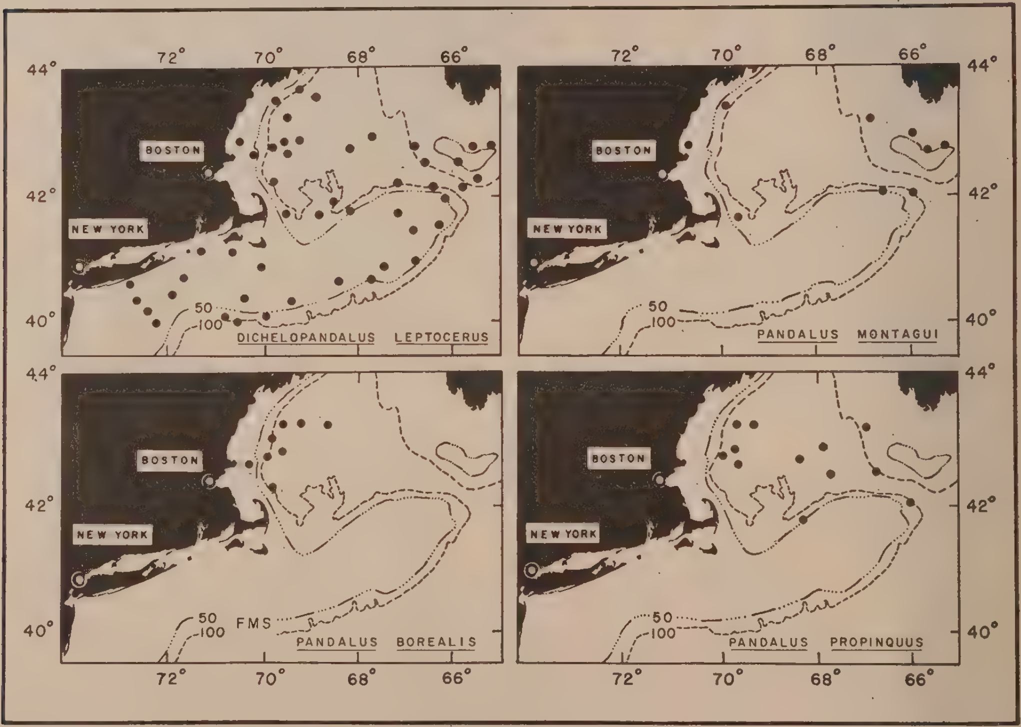
72°
70°
68°
66°
44°
42°
40°
BOSTON
NEW YORK
50
100
FMS
DICHELOPANDALUS LEPTOCERUS
PANDALUS MONTAGUI
PANDALUS BOREALIS
PANDALUS PROPINQUUS

FIG. 2. Geographic occurrence of the four most common species of New England pandalid shrimps, November 1956. Each dot represents a trawling station at which one or more specimens were caught.

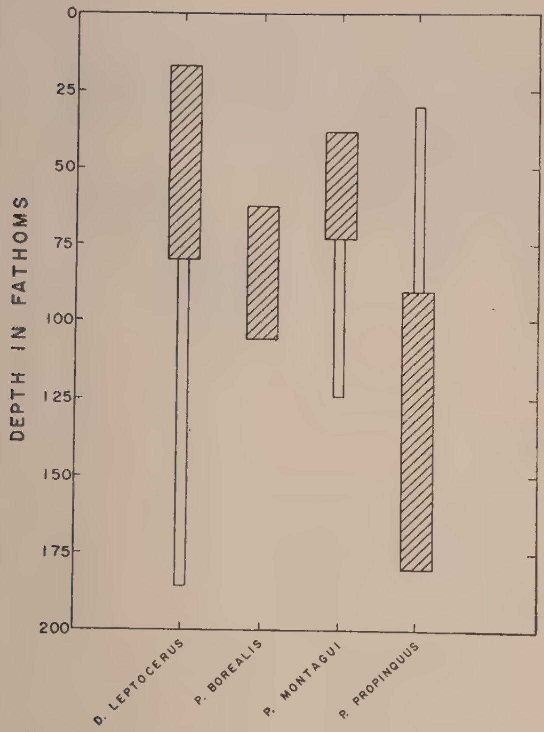

Fig. 3. Species occurrence in relation to water depth. Wide bar denotes 90 percent or more of the specimens; narrow bar denotes 10 percent or less.

Bigelow and Schroeder 1939; Whiteley 1948; Scattergood 1952) pertaining to the New England distribution of pandalid shrimps considered in this report has revealed rather few specific records of occurrence. The older publications usually cite few occurrence records and list them by species, whereas many of the more recent reports list more localities but group the species by genera or family. This literature is effectively summarized, in respect to geographic and bathymetric ranges, by M. J. Rathbun (1929) as follows:

Species	*Geographic range in western Atlantic Ocean*	*Bathymetric range (fathoms)*
Dichelopandalus leptocerus	Newfoundland banks to North Carolina	7-430
Pandalus borealis	Greenland to Cape Cod, Massachusetts	20-495
Pandalus montagui	Greenland to Rhode Island	3-430
Pandalus propinquus	Newfoundland banks to Delaware	34-1,089

MATERIALS AND METHODS

New occurrence records given in this report are based on collections taken November 2-20, 1956, during a groundfish survey conducted by the U. S. Fish and Wildlife Service, Woods Hole, Massachusetts. Collections of shrimp were made by personnel aboard the *Albatross III*, Cruises 81 and 82, at 54 of the 95 stations occupied in offshore waters on the continental shelf from Long Island northward to central Gulf of Maine and eastward to Cape Sable, Nova Scotia (Figure 1). Station data and collection records are listed in Table I.

A No. 36 otter trawl with an 80-foot groundrope and wooden rollers, plus the addition of a partial liner of ½-inch (extension measure) mesh, was employed in making all catches. Since this trawl is not designed for capturing shrimp, the numbers taken are probably minimal estimates of abundance. A standard tow of one-half hour duration was made at most stations. In the few cases where longer tows were made, catches were adjusted to the standard one-half hour period. The shrimp were preserved at sea and brought to the laboratory for identification.

Water depths were measured by means of a Bendix recording fathometer. The depths recorded in Table I are average values of the maximum and minimum soundings registered during each tow. A bathythermograph was used to determine bottom temperature. The temperature records, also included in Table I, are available for approximately 80% of the stations occupied.

I wish to thank Dr. John T. Conover, formerly with the U. S. Fish and Wildlife Service, and other staff members who collected the specimens and kindly placed them at my disposal.

RESULTS

Geographic Distribution

Catch records for the four species of pandalid shrimps are listed separately in Table I. The geographic occurrence of each species is illustrated in Figure 2. It is apparent from these charts that at this time of year each species has a characteristic geographic distribution. *D. leptocerus* is widely distributed over the entire area. This species is the only one common on Georges Bank and south of Cape Cod. *P. borealis* was taken only in a limited area in central and western Gulf of Maine. Of the 4 species, it has the most restricted geographic distribution within the study area. (Only 13 specimens of *P. borealis* were collected at 8 stations; therefore, the conclusions drawn for this species must be considered tentative.) *P. montagui* occurred around the perimeter of the Gulf of Maine with greatest numbers taken in the vicinity of Browns Bank. *P. propinquus* was found in the central Gulf of Maine and along the northern edge of Georges Bank. Since *D. leptocerus* inhabits the entire area sampled, it thus occurs at the same localities with the other 3 species. The distributions of the 3 species of *Pandalus* overlap one another along the fringes of their centers of abundance.

Bathymetric Distribution

The species distribution charts (Fig. 2), in which the 50-and 100-fathom isobaths are drawn, suggest that the geographic distribution of each species is related to water depth. This relationship is illustrated more clearly in Figure 3, a bar graph depicting species occurrence in relation to water depth. This illustration reveals that *D. leptocerus* inhabits a comparatively wide range in depth, from 18 to 186 fathoms. However, this species was most common in shallow and moderately shallow waters, between 18 and 80 fathoms, and was the only pandalid taken in water depths less than 30 fathoms. *P. borealis* occupied a relatively narrow stratum in moderately deep water. It was found only in depths between 62 and 106 fathoms. *P. montagui* was most common in depths between 38 and 73 fathoms, with 3 speci-

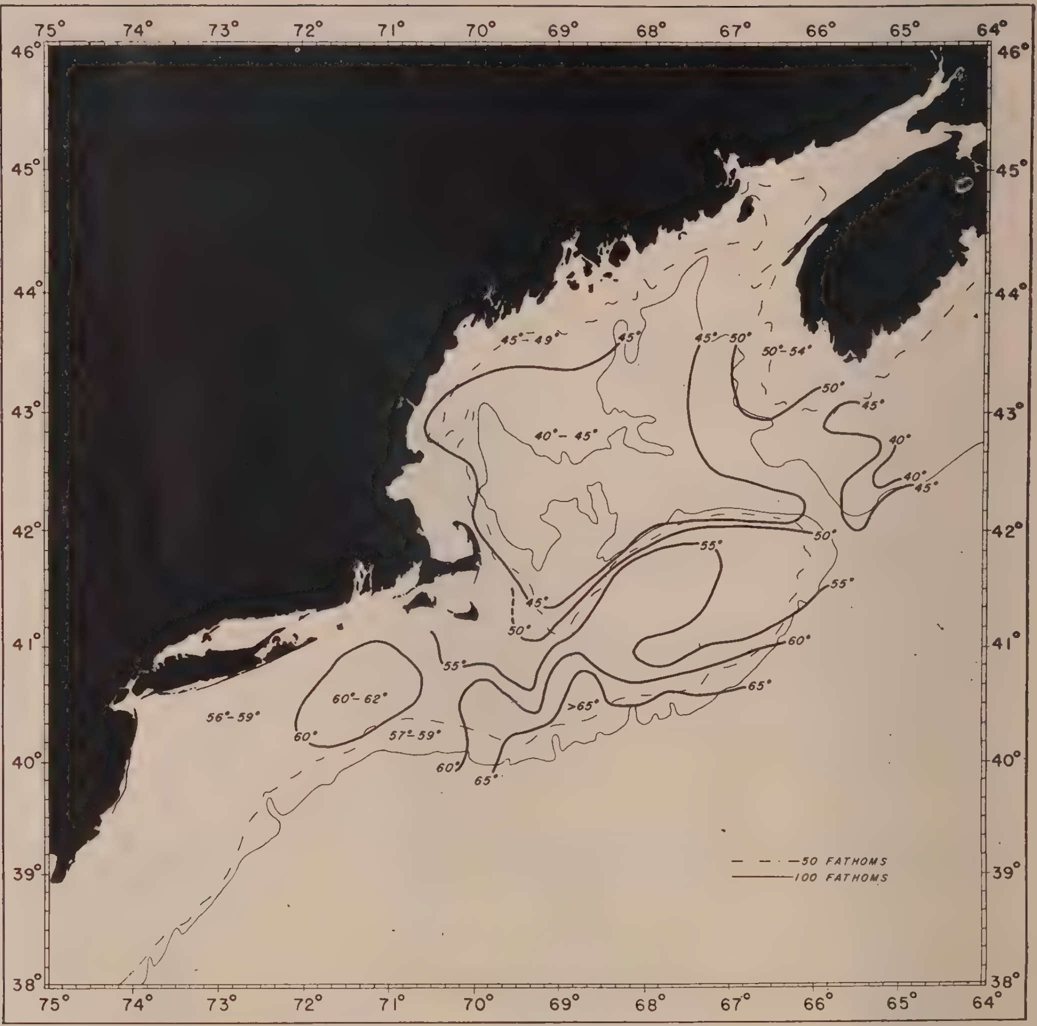

FIG. 4. Bottom water temperature in degrees Fahrenheit, November 1956.

mens occurring as deep as 124 fathoms. *P. propinquus* is a relatively deep water inhabitant and commonly occurred in waters between 90 and 180 fathoms in depth. One specimen of this species was found in 30 fathoms.

To summarize briefly, these catch records disclose that during November, *D. leptocerus* was most commonly found in shallow and moderately deep water. *P. borealis* and *P. montagui* were most abundant at moderate depths. *P. propinquus* was most common in relatively deep water. There were no pronounced diurnal differences in the catch for any of the 4 species.

Temperature Relationships

Pandalid shrimps in New England waters may be restricted in their geographic distribution by temperature barriers. The relationship between water temperature and occurrence of these shrimps, by species, may be examined from 2 aspects: (1) a comparison of geographic distribution with bottom water isotherms, and (2) a comparison of ranges in water temperature at specific localities where each species occurred.

Isotherms of bottom water, based on measurements taken at trawling stations and at 57 intermediate locations, are plotted in Figure 4. This figure discloses the presence of a sharp temperature gradient along the northern border of Georges Bank. The 45°F and 50°F isotherms are closely adjacent on this edge of the bank. A comparison of the geographic distribution of each species of shrimp (Fig. 2) with the temperature isotherms (Fig. 4) reveals several interesting facts. It may be observed that *Pandalus* was not taken south of this zone of pronounced temperature change. Possibly the 50°F isotherm acts as a barrier to the southward spread of *Pandalus.*

Water temperature apparently has little effect on the distribution of *Dichelopandalus* under the conditions existing at the time and places these collections were made. However, isotherms of bottom water suggest that temperature may influence the distribution of species of *Pandalus,* but this is brought out more clearly in the following discussion.

The range in water temperature in which each species

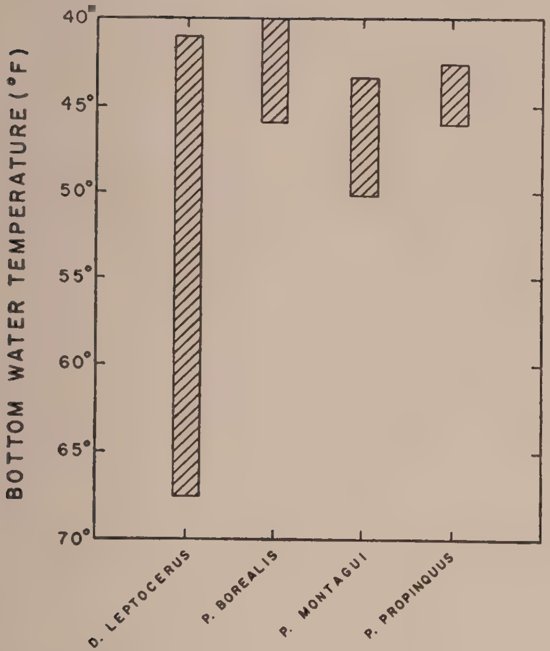

FIG. 5. Range in bottom water temperature (°F.) associated with each species of shrimp.

of shrimp was found is illustrated in Figure 5. This graph serves to emphasize 2 points. (1) It clearly reveals the wide temperature range, from 41° to 68°F, inhabited by *D. leptocerus.* (2) It illustrates the colder and relatively narrower range in temperature associated with all 3 species of *Pandalus;* all occur within a range of 40°-50°F. Comparatively small differences in temperature ranges among these 3 species are evident. *P. borealis* was taken in the coldest waters, 40°-46°F. *P. propinquus* was found in slightly warmer waters, 43°-46°F. *P. montagui* occurred in still warmer waters, 43°-50°F.

Bottom Sediment Relationships

It is an established fact that bottom sediments have a significant influence on the occurrence of many benthonic marine organisms. This dependency on sediment varies according to the animal's habits and requirements. Pandalids feed on living or dead plants or animals; therefore, the associations between species-occurrence and sediment-type may be either a direct or indirect relationship, or a combination of both. A distinct relationship between abundance of pandalid shrimp and the amount of organic matter in the sediment has been demonstrated by Hjort and Ruud (1938) and Bigelow and Schroeder (1939). Referring primarily to *P. borealis* in Gulf of Maine waters, Bigelow and Schroeder found these shrimp to be most abundant where the sediment organic content averaged 4.0%. In adjacent localities where the organic content averaged 3.0%, these shrimp were definitely less common.

New information on this subject is presented here, pertaining to pandalids in the vicinity of Georges Bank. Sediment samples from 223 localities on or near Georges Bank were analyzed for organic content.[1] The quantitative geographic distribution of sediment organic content based on these samples is illustrated in Figure 6. A comparison of pandalid distributions (Fig. 2) with the distribution of sediment organic content reveals 2 points of interest. First, it substantiates previous findings that *Pandalus borealis* is not common where sediment organic matter is low. Secondly, it indicates that *Dichelopandalus* is less restricted than *Pandalus* in this respect. *D. leptocerus* was usually more abundant where the sediment organic content was greater than 0.5%, but it was prevalent over a large area where the organic content was very low, 0.5 to less than 0.1%.

In regard to *P. montagui* and *P. propinquus,* the evidence is less conclusive. *P. montagui* was found to occur at a few localities where the sediment organic content was very low (less than 0.1%) and it was not taken where the organic content is known to be high (3 to 4%). *P. propinquus* was collected over diverse sediment types representing a wide range in sediment organic content. In some localities where this species was taken, the organic content was low, but it was most common where the organic content was at an intermediate or high level.

SUMMARY

The 4 species of Pandalidae common in New England offshore waters are: *Dichelopandalus leptocerus* (Smith), *Pandalus borealis* Kröyer, *Pandalus montagui* Leach, and *Pandalus propinquus* G. O. Sars.

Otter trawl catches of these shrimps in November 1956, in the area from Long Island northward to the central Gulf of Maine and eastward to Cape Sable, Nova Scotia, reveal some distinct relationships between species distribution and environmental factors.

Dichelopandalus leptocerus was ubiquitous over the entire study area and was taken in a wide range of water depths (20 to 190 fathoms) and a broad range in temperatures (41° to 68° F). It was common over sediments containing low, medium and high quantities of organic matter.

Pandalus borealis occurred in a limited portion of central and western Gulf of Maine. It was found only in waters of moderate (60 to 110 fathoms) depth, rather low temperatures (40° to 46°F), and over sediments high in organic content.

Pandalus montagui inhabited the periphery of the Gulf of Maine basin. This species was most common in moderate depths (40 to 70 fathoms), moderately low temperatures (43° to 50°F), and appeared to be associated with sediments relatively low in organic content.

Pandalus propinquus occupied the central Gulf of Maine basin. It was usually found in deep (90 to 180 fathoms), moderately cold (43° to 46°F) water, and was most common over sediments containing medium or high quantities of organic matter.

Diurnal periodicity of occurrence in the catch was not apparent for any of the 4 species.

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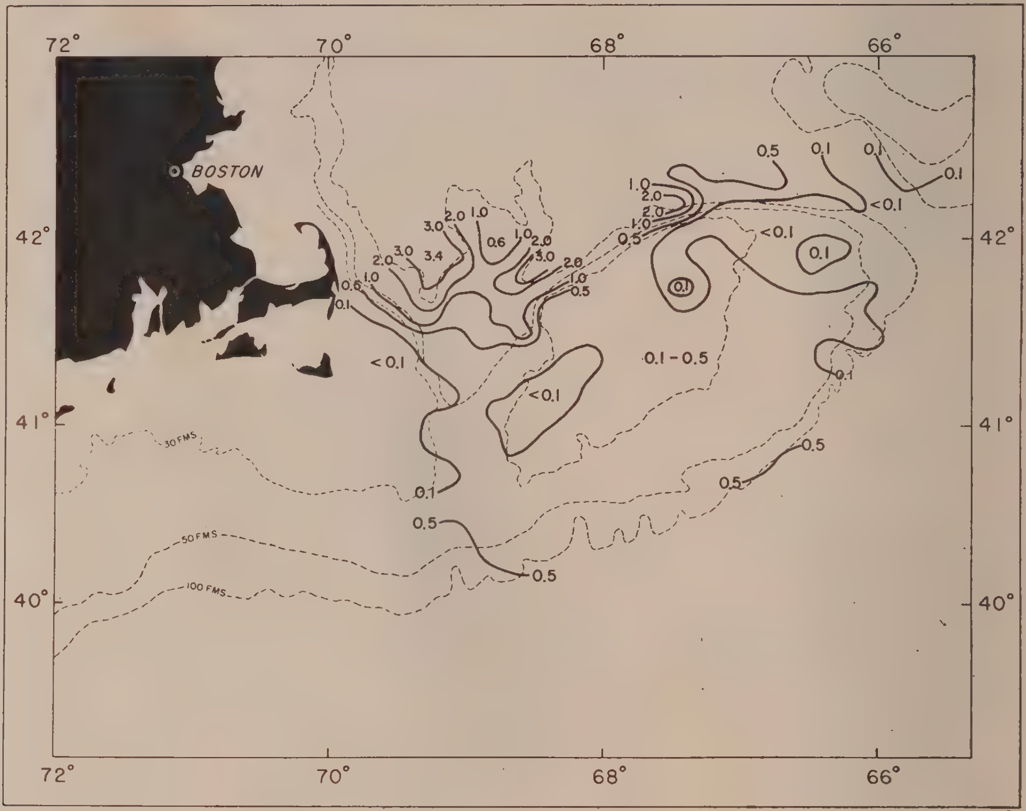

FIG. 6. Geographic distribution of organic matter in sediments on Georges Bank and vicinity. Values are given in percentage weight.

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THE SMALL MAMMAL COMPONENTS OF SIX CLIMAX PLANT ASSOCIATIONS IN EASTERN WASHINGTON AND NORTHERN IDAHO[1]

INTRODUCTION

The vegetation of eastern Washington and northern Idaho includes semi-desert, grassland, and coniferous forest (Daubenmire 1942, 1952). In this region Rickard (1960) sampled quantitatively the small mammal components of 14 climax plant associations. The present study was aimed at determining the small mammal components of 6 additional plant associations not sampled by Rickard.

VEGETATION

The 6 plant associations studied are all within the forested area, (see Table I). Four of the associations dominated by coniferous trees have already been characterized (Daubenmire 1952), so that only the other 2 associations need be described here.

TABLE I. The plant associations studied and their locations

Plant association	Location
Pinus ponderosa/Agropyron spicatum	Spokane County, Washington R43E, T24N, S33
Pseudotsuga menziesii/Calamagrostis rubescens	Bonner County, Idaho R5W, T54N, S28
Thuja plicata—Tsuga heterophylla/Pachistima myrsinites	Bonner County, Idaho R5W, T62N, S29
Thuja plicata—Tsuga heterophylla/Oplopanax horridum	Pend Oreille County, Washington R45E, T38N, S17
Alnus sinuata	Latah County, Idaho R4W, T40N, S17
Carex lasiocarpa	Bonner County, Idaho R5W, T60N, S11

Small dense climax stands of *Alnus sinuata* (Regel) Rybd. occur throughout the Northern Rockies. The one used for this study is on a northeast facing slope of Moscow Mountain near Moscow, Idaho. Because of the weight of accumulated snow during winter and the incomplete springing-up of the trees during spring thaw, the stems are all prostrate at the base with the ascending tips pointing downslope. A small stream runs the course of the thicket and the herbaceous undergrowth is dense. Conspicuous undergrowth plants include *Athyrium filix-femina* (L.) Roth., *Mertensia paniculata* (Ait.) G. Don., *Clintonia uniflora* (Schult.) Kimth., *Claytonia sibirica* L., and *Veratrum viride* Alt.

Also interrupting the continuity of the conifer forests are a number of fens dominated by species of *Carex*, *Spiraea*, *Betula*, and *Salix*. An area selected for sampling, approximately 8 km south of Nordman, Idaho, was composed chiefly of *Carex lasiocarpa* (Ehrh.) which forms a very dense herbaceous cover near the ground. In localized patches bordering the *Carex* stand are thickets of *Spiraea douglasii* (Hook.) as well as some *Betula* and *Salix*.

METHODS

All trapping was done in 1958 during the months of June, July, and August. To provide directly comparable results, the methods in this study were identical to those of Rickard (1960). A trapping period consisted of 3 consecutive 24 hour periods and, except for the stand representing the *Thuja-Tsuga/Oplopanax* association, each study site was trapped during each of the 3 months. The trapping grid consisted of 3 trap-lines of 5 stakes each, the lines and stakes being placed 8 meters apart. Three spring traps of the house mouse variety were placed about each stake. Bait consisted of a mixture of oatmeal and peanut butter. One exception to the above method was necessary, because of the elongate form of the *Alnus sinuata* thicket, a single trap-line of 15 stakes was placed down the center. All stands accepted for study exceeded 2 acres and trapping grids were placed well within each stand of vegetation so as to minimize the influences of ecotones and roads or other disturbed areas.

In one stand representing the *Thuja-Tsuga/Pachistima* association 2 trapping grids were placed approximately 200 meters apart. This was to determine the extent of variations that might be expected within a single large stand of vegetation.

RESULTS AND DISCUSSION

A total of 2700 trap days yielded 110 specimens of 11 species of small mammals in the 6 plant associations (see Table II).

TABLE II. Results of sampling six plant associations in eastern Washington and northern Idaho showing the numbers of the small mammals captured in 405 trap days

Zone	Plant association	*Peromyscus maniculatus*	*Sorex vagrans*	*Sorex cinereus*	*Sorex obscurus*	*Phenacomys intermedius*	*Eutamias amoenus*	*Eutamias ruficaudus*	*Clethrionomys gapperi*	*Zapus princeps*	*Microtus montanus*	*Microtus pennsylvanicus*
Pinus ponderosa	*Pinus/Agropyron*	9										
Pseudotsuga	*Pseudotsuga/Calamagrostis*		1									
Thuja—Tsuga	*Thuja—Tsuga/Pachistima* (a)	3	2	2		1						
	Thuja—Tsuga/Pachistima (b)	3	2	1	1		1					
	*Thuja—Tsuga/Oplopanax**	1	1			1	1		2			
	Alnus	5	3					1	9	2	3	
	Carex		19									36

* Numbers for this stand represent only 270 trap-days.

Peromyscus maniculatus (Wagner) was trapped in 4 of the associations and was the only species taken in the savanna-like stand of *Pinus/Agropyron* (Table II). Though Bailey (1936) suggests that this mouse is mainly characteristic of semi-arid regions with open timber and brush being its main habitat, it has since been demonstrated that *P. maniculatus* is common in a wide variety of habitats ranging from grassland devoid of shrubs to dense mesophytic forest (Manville 1949, Williams 1955, Rickard 1960).

Microtus pennsylvanicus (Ord) was present only in the very moist *Carex* fen, but here it was very abundant. Judging from other studies the population density of this mouse seems to be directly related to the amount of protective cover at the ground (Griffenius 1939, Eadie 1953, Morris 1955). But since this mouse was not trapped in the *Festuca/Symphoricarpos* association (Rickard

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[1] The writer wishes to thank Dr. R. Daubenmire for the many helpful suggestions made throughout the course of this study.

1960) which also provides dense vegetative cover, its distribution may also be limited by the availability of free water throughout the summer. It is significant that, according to Davis (1939), the range of *M. pennsylvanicus* has been extended due to irrigation, so that it is now commonly found in hayfields, pastures, and along irrigation ditches.

Sorex vagrams (Baird) was absent only from the *Pinus/Agropyron* association. Rickard (1960) found its apparent lower phytosociologic limit in this region to be the *Festuca/Symphoricarpos* association which in some respects is less xerophytic than the *Pinus ponderosa/Agropyron* forest. The same dense herbaceous vegetation preferred by *Microtus pennsylvanicus* also appears to be the most favorable habitat for *Sorex vagrans* (Davis 1939, Clothier 1955).

Sorex cinereus (Kerr) and *S. obscurus* (Merriam) were trapped infrequently but always in forest vegetation where the *Pachistima* union is represented, this bearing out Rickard's (1960) results.

It is well known that the distribution of *Clethrionomys gapperi* (Rhoads) is related to the extent of coniferous forests, however its distribution within the forest is uneven and is apparently influenced by local conditions of suitable cover and availability of free water (Butsch 1954, Rickard 1960). In the present catch *Clethrionomys* was represented only in 2 moist habitats, *Thuja-Tsuga/Oplopanax*, and *Alnus sinuata.* Its relative abundance in the latter habitat seems to bear out comments by Butsch (1954) that the local distribution of *Clethrionomys* may be controlled more by the availability of free water rather than by suitable food.

Two chipmunks, *Eutamias amoenus* (Allen) and *E. ruficaudus* (Howell) were represented in the catch. Rickard (1960) trapped *E. amoenus* in nearly every stand of vegetation dominated by coniferus trees. *E. ruficaudus,* represented in the present catch only in the moist deciduous alder thicket, was not trapped in any of the vegetation types sampled by Rickard (1960). Dalquest (1948), however, reports that he could detect no difference in habit or habitat of the 2 species.

Another animal found in the coniferous forests was *Phenacomys intermedius* (Merriam). This species, and also *Zapus princeps* (Davis) were not taken in any of the plant associations sampled by Rickard (1960). Davis (1939) records *Z. princeps* as being present in communities of ponderosa pine, Douglas fir, willow and alder, although the successional status and moisture relations of these communities cannot be inferred from his comments. *Microtus montanus* (Peale), previously found only in climax grassland of the *Festuca* zone (Rickard 1960) is also present in the Alnus association.

The 2 trapping sites within the single stand of the *Thuja-Tsuga/Pachistima* yielded closely similar results. Reproducibility of results for the method of sampling was demonstrated by Rickard (1960) who found that conclusions based on analyses made in consecutive summers were essentially identical.

SUMMARY

Six plant associations were sampled for their small mammal components, using methods identical to those of Rickard (1960) who studied 14 associations in the same region. Four additions were made to the list of species known to inhabit climax communities, and the known vegetational preferences of other species extended. In one test made in different parts of the same stand of forest the sampling method yielded closely similar results.

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A NEW AND SIMPLE METHOD FOR THE ISOLATION OF FRESH-WATER INVERTEBRATES FROM SOIL SAMPLES

Introduction

Bidlingmayer (1957) discussed techniques of isolating *Culicoides* larvae from brackish soil. Among these was one, considered by him to be the most satisfactory from the standpoint of time and convenience, of placing a 2 inch layer of builder's sand on top of a soil sample and flooding with water. The following day, after placing the sand in a dishpan, it was washed and the wash water was poured through a 140-mesh screen and the residue (containing the larvae) was then washed into a black photographic developing tray. The light colored larvae could be seen swimming against the dark background and removed with a siphon. Bidlingmayer also recovered some annelids and crustaceans from brackish soils using this technique.

The principle of washing sand, filtering, and pouring or rewashing the residue into a pan for examination has been used for many years by limnologists for the isolation of midge larvae, and other animal life, from the psammolittoral of lakes and was mentioned briefly by Williams (1955). Bidlingmayer's extremely important contribution in the use of this established technique was to show that it could be used successfully for the isolation of midge larvae which were found in other than sandy soils and that these larvae migrated from their normal soil habitat into the sand above.

This technique was utilized for the isolation of fresh-water *Culicoides* and other midge larvae in northern Michigan during the summer of 1959. At this time it was observed that it was an excellent technique for isolating numerous invertebrate groups from other than sandy soil. Since this technique is relatively new and since it has not been reported as being used for fresh-water forms it is not generally recognized by fresh-water biologists and invertebrate zoologists as a tool which can be of great assistance in their collecting. It was therefore felt that its use for this purpose should be reported.

Isolation Techniques

A round soil sample approximately 2 inches (5.08 cm) thick was cut to fit the bottom of a container having an area of 64 sq. inches (412.8 cu. cm) (any size soil sample may be used). Two inches of dry sand, taken from top sand well back in the eupsammon of a lake, were placed on top of the sample and the sample and sand flooded with water. After standing overnight (20 to 27 hours), a portion of the sand was scooped into a 200 mm biological specimen dish and washed by forcing a jet of water through the sand thus stirring it. The water was immediately poured through a 120-mesh plankton net and the sand in the dish again washed and this water poured through the net. The net was then inverted over a photographic tray and the residue, with invertebrates, washed into the tray. These steps were repeated until all of the sand that could be scooped from above the soil sample had been processed. The water, which nearly filled the photographic tray, was again poured through the plankton net and the residue again washed back into the tray with one glassful of water (8 ozs.-.284 litres), thus greatly reducing the amount of water to be examined. The water from the tray was examined in 4 examinations in a 112 mm biological specimen dish, the outside bottom of which had been divided with a glass marking pencil into fourths and two concentric circles. The distance between the circles and from the edge of the dish to the first circle was equal to the diameter of the low power field of a dissecting microscope. Wiggling larvae, and other visible forms, were pipetted off and then the dish placed under the microscope and the contents examined. In this manner any forms, living or dead, hidden in debris could be seen and flushed out with a pipette for collection.

Some bog-mat samples contained numerous small particles of peat which would float in the process of depositing the sand upon the sample. These particles would be removed with the sand and appear on the filter and in the photographic tray. In certain samples these particles would be so numerous that they would completely cut out the passage of light through the bottom of the biological specimen dish. When such samples were encountered, a saturated solution of $MgSO_4$ (one 8-10 oz. glassful) was used to wash the residue from the plankton net in the process of reducing the amount of liquid to be examined. When the contents of the dish were stirred the invertebrates would float to the top because of the high specific gravity of the $MgSO_4$ solution, while the peat particles would gradually settle out. The contents of such a dish were stirred and re-examined until 3 consecutive negatives occurred.

Invertebrate Groups Isolated from Fresh-Water Soil Samples

The kind and number of invertebrates recovered would, of course, vary with the soil type and sample. Since no attempt was made to keep a record of the numbers of each group recovered from each sample and area the comments presented herewith refer to all samples collectively.

The following groups of fresh-water invertebrates were found to leave their normal soil habitat and migrate into the sand above, from which they were readily isolated: Coelenterata, Turbellaria, Nematoda, Oligochaeta, Ostracoda, Acarina, Diptera larvae, Gastropoda, and Plecypoda. Of the Turbellaria, for example, representatives of 5 genera from 3 families and 3 orders were collected from 3 collecting sites. Included in this group was the genus *Prorhynchus*, from Reese's Bog, Cheyboygan Co., Michigan, identified by Professor Frank E. Eggleton of the University of Michigan Zoology Department. According to Professor Eggleton, this genus had not previously been collected or reported in the State of Michigan. Many of the above named groups would at times be found in considerable numbers in certain samples.

The reason for the migration of these animals into the sand above their usual soil habitat is not known but may be due to a change in oxygen tension within the normal habitat caused by the sand layer. It may, therefore, be probable that any minute soil-inhabiting metazoan animal can be collected by this technique.

Summary

A technique described by Bidlingmayer (1957) for the isolation of brackish water *Culicoides* larvae was found to be a useful one for the isolation of numerous fresh-water invertebrates from various types of soils. The technique is one not generally recognized by fresh-water

biologists and invertebrate zoologists. Results indicate that it is a very useful procedure, with modifications when necessary, for the collecting of Coelenterata, Turbellaria, Nematoda, Oligochaeta, Ostracoda, Acarina, Diptera larvae, Gastropoda, Pelecypoda, and possibly other groups.

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ESTIMATION OF A LOUISIANA POPULATION OF THE SKINK, *LYGOSOMA LATERALE*[1]

The determination of numbers of reptiles is a part of the broader problem set forth by Fitch (1949) and Cagle (1953) in their outlines for the study of reptilian life histories. Specifically, estimates of numbers are involved in analysis of the densities, age-compositions and sex-ratios of populations, and the quantitative behavior of populations resulting from natality and mortality. These specific problems cannot really be attacked effectively without means of obtaining reliable population estimates.

It is surprising, then, to find that the sizes of lizard populations have been almost invariably taken simply as the number of individuals which could be captured and marked by repeated sampling (*e.g.* Fitch 1940, 1956, 1958; Miller 1944, Stebbins 1944, 1948; Stebbins and Robinson 1946, and Crenshaw 1955). Sometimes the estimate is qualified as a minimal estimate and sometimes it is not. It must be conceded that continued collecting and marking by an experienced investigator, especially of a conspicuous diurnal species (*e.g. Sceloporus* sp. or *Crotaphytus* sp.), will result in the tabulation of a high percentage of the population. Basically, the success of this procedure hinges on the design of the field work, the experience and judgment of the investigator, and the habits of the lizards involved. This is not a particularly satisfactory situation, but there seems to have been little effort made to develop more standardized means of determining the numbers of lizards. Since it is known that there are behavioral differences between males and females and between adults and young which affect susceptibility to capture, it is evident that the analysis of such data must be carried out with caution.

Ideally, we need some method of estimation which is reliable in the hands of the neophyte, which will not be influenced by marked differences in the susceptibility to capture of different age groups, and which does not depend on observations or samples continued over a period of months or years. The most obvious method would seem to be some application of capture-recapture technique, though under some conditions a partial removal program suggests itself. If it is desired to leave the population undisturbed it may be possible to keep the captured animals and release them, at the point of original capture, after the removal program is completed. This last does not differ qualitatively from a program of continued marking and recapture but is advantageous in that it may be compressed into a relatively short span of time. Theoretically, it is not necessary to remove the entire population to estimate its size. Zippin (1958) has presented a simplified explanation of the estimation of numbers from as few as 2 consecutive samples.

In the present study, an attempt has been made to estimate the size of what seemed to be a relatively isolated population of skinks (*Lygosoma laterale*) inhabiting the west end of a field 5 miles south of Covington, St. Tammany Parish, Louisiana. A capture-recapture procedure and analysis as described originally by Schumacher and Eschmeyer (1943) and more recently by Hayne (1949) and DeLury (1958) has been used. The removal method, based on 3 collections, has also been tested.

The habits of little brown skinks have been well documented by other authors. The lizards are small, somewhat secretive, and elusive. In the area studied they retire at night to the duff underlying the wooded border of the field (loblolly pine, sweet gum, bayberry) and forage in the open areas during most of the day. They rarely venture far from the edge (see Figure 1, illustrating the distribution of all captures and recaptures), and when alarmed scurry quickly for the cover of the 2″-thick duff of pine needles, dead twigs and leaves. Attempting to capture these small lizards would be instructive for those doubting the selective value of autotomy.

Methods

Skinks were caught by hand, a procedure at which one becomes progressively more skilled, up to a point. Towards the end of the study I caught about half of the skinks which were observed. Captured individuals were marked by clipping varying numbers and combinations of toes and then released. The point of capture was marked on a 5-meter grid map of the area. Natural loss of toes occurs fairly commonly and there were occasional uncertainties as to whether lizards were marked or unmarked. Lizards were collected and released on March 27, 29, 30, 31, and April 1, 1959. On April 2, 3, and 4, lizards were collected as efficiently as possible between 10 A.M. and noon and retained. On the last 3 dates, a GE exposure meter was set up at one edge of the field and readings were taken at half-hour intervals. Ground temperatures and air temperatures were also taken at half-hour intervals. The area was circled slowly in searching for skinks. About 15 circuits were made in 2 hours.

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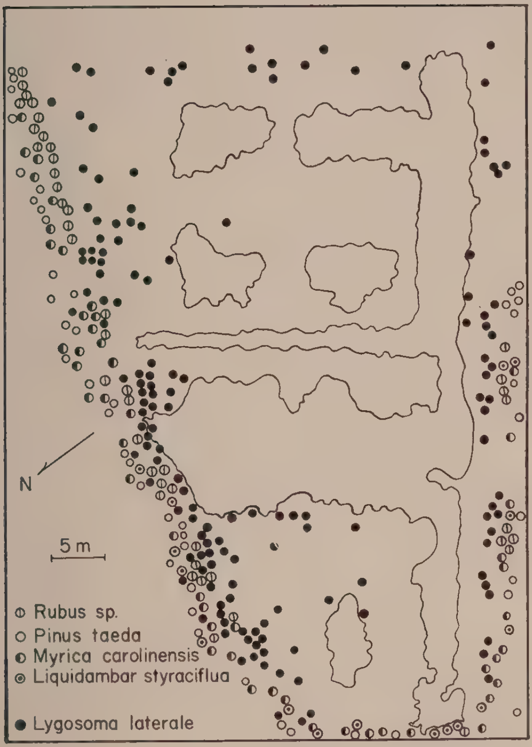

FIG. 1. Field in St. Tammany Parish, Louisiana, showing vegetational border, captures and recaptures of skinks, and standing water.

TABLE I. Recapture data from a Louisiana population of *Lygosoma laterale*

Date	Total number captured	Marked individuals recaptured
March 27	26	—
29	14	1
30	30	7
31	7	3
April 1	13	7
2	32	11

CAPTURE-RECAPTURE ANALYSIS

The capture-recapture data through April 2 are summarized in Table I. The applicability of the Schumacher method depends on the assumption of a stable population. If this assumption is realized the proportion of each catch which has been previously marked should increase regularly (Hayne 1949). In the present data these proportions increase from .07 on March 27 to .54 on April 1, but on April 2 only .34 of the catch had been marked previously. This last proportion implies dilution of the population by unmarked individuals. On the other hand, a test of dilution as suggested by Leslie (1952) gives a quite insignificant Chi-square (5.365 with 10 degrees of freedom) which indicates that there was no significant dilution. The Schumacher estimate, with the data from April 2 included, is 175 with a 95% confidence range of 130 to 267 (calculated as described by DeLury 1958). With the data from April 2 omitted the estimate is 146 (105-240).

ESTIMATE BY REMOVAL METHOD

On April 2, 32 skinks were caught between 10 A.M. and noon. In the same 2-hour interval on April 3, 18 were captured, and on April 4, 16 were taken. The method outlined by Zippin (1958) yields a population estimate of 100 with a standard error of 23.0.

DISCUSSION

Toe-clipping is not as reliable a method of permanent marking as tattooing, but is the most feasible method usually available. I recommend cutting one toe from each foot. Toe loss is common in little brown skinks but if the above system is used there is little possibility of confusing marked animals with unmarked. Loss of digits apparently does not influence mortality to a significant degree in a short-range study. Lizards with missing feet (and one with only 3 legs) were observed and their agility was unimpaired.

There is some uncertainty as to the validity of the capture-recapture analysis implied by the composition of the sample of April 2. The lower percentage of marked individuals taken in the sample of 32 skinks collected on this date may be partially explained by considering the source of this sample in detail. By referring to Fig. 1, one may observe that about 66% of the lizards captured were taken along the north side of the field, about 22% along the south side, and the remainder were scattered along the east edge of the study area or toward the center of the field. This is partly due to unequal distribution of effort (through April 1), and partly due to an actual difference in numbers. There may also have been, through April 1, a difference in collecting efficiency on the 2 sides of the field. The area utilized along the south side is narrower than along the north side (Fig. 1), and hence the foraging lizards were closer to cover on the south side and escaped more easily when alarmed. At any rate, until April 2, only 11 lizards had been captured along the south edge, while in the same interval 72 had been taken on the north side. On April 2, 11 of the entire sample of 32 were taken along the south edge and of these 11, 10 were unmarked. This resulted in a marked increase in the proportion of unmarked individuals in the April 2 sample. This suggests treating the subpopulations on the north and south side of the field separately. This procedure is justified because the recaptures of marked skinks indicate very low vagility. Of 37 movements recorded, 14 were of less than 2.5 m, and 16 were between 2.5 and 5 m. Indeed, 24 of the 30 marked individuals recaptured during the entire study were recaptured within 5 m of the point of original capture. Such well-defined activity ranges seem to be generally characteristic of lizards, although these areas are ordinarily much more extensive than those of *Lygosoma* (Fitch 1940, 1958; Stebbins and Robinson 1946). When data for the north side are extracted, the proportions of marked individuals increase as follows: .08, .24, .60, .63, up through April 1. There is then a drop to .48 on April 2, but now this sample is not so far out of line. The Schumacher estimate of the north side population is 114 (95% confidence limits of 84 and 174) including data from April 2, and 108 omitting the data from April 2. The remaining capture-recapture data, involving individuals from the south side, are scanty but an estimate of numbers may be made by the proportional index. On April 2, with 10 marked animals at risk along the south side, a sample of 11 lizards contained but one marked. With Bailey's (1952) correction for bias these figures give an estimate of 60 with a standard error of 31.7. The separate estimates of the lizards along the north and south sides suggest that no serious error will be introduced by adopting the original estimate of 175 (130-267) for the entire population, which utilizes all available recapture data.

At one point in the experiment the question arose as to whether the time of day at which collections were made would influence the composition of samples. Could there be various segments of the population utilizing the available habitat in rotation? This apparently may occur in spadefoot toads (Pearson 1955), with obvious disadvantages as far as capture-recapture analyses are concerned. If this were so in the *Lygosoma* popualtion samples drawn in the morning might actually be taken from a different subpopulation than samples taken in the afternoon. The collections of March 29 and April 1 were made in the afternoon (2-4:30) while the rest of the samples were taken in the morning (9-12 more or less). It is possible then (assuming all marked individuals to be equally susceptible to capture), to calculate the expected proportions of individuals marked in the morning and afternoon in the total array of marked animals recaptured on March 30 and thereafter (Table II). A Chi-square test of the totals yields a value of .94 which gives no reason to suspect that individuals marked at one time of day are less susceptible to recapture at another.

TABLE II. Comparison of recaptures of skinks originally marked in the morning as opposed to those marked in the afternoon

Date	Total at Risk Just Prior to Sampling		Total re-captures	Time Recaptured Individuals Were Originally Marked			
	Marked in morning	Marked in afternoon		Morning		Afternoon	
				Actual	Expected	Actual	Expected
March 30...	26	13	7	6	4.67	1	2.33
31...	49	13	3	3	2.37	0	0.63
April 1...	53	13	5	4	4.02	1	0.98
2...	53	19	8	6	5.89	2	2.11
			Totals	19	16.95	4	6.05

It is not possible to determine whether marked animals become wary and less likely to be captured. Certainly this has proved to be the case with *Sceloporus* (Fitch 1940, Stebbins 1944). If this proves to be a regular problem with lizards, capture-recapture methods will be apt to overestimate population size. Fitch (*in litt.*) has pointed out that the converse problem may also exist, *i.e.* marked animals may be less wary and hence more susceptible to capture.

In the application of the removal method it is imperative that the effort be uniform from one sampling to the next. This is presumably achieved in studies of mammalian populations by the use of the same number of traps over identical periods of time. In studies of lizards an arrangement of this nature would rarely be practical. Usually the collections are made by hand or with various adjuncts such as nooses, rubber-bands, or corral-traps so there is cause to doubt the possibility of achieving equal effort over a number of samplings. Secondly, the activity of members of the population, and their susceptibility to capture, must be assumed constant over the sampling periods. In the case of lizards and other ectotherms this assumption demands uniform conditions of temperature and probably illuminance, preferably coupled with lack of rain. Finally, it is necessary that the population studied be isolated, or the species of low mobility, so that no replacement of removed individuals occurs. The outlook for the use of the removal method to estimate lizard populations on the basis of, say, 3 to 7 samplings, is not promising. In the present study, however, the conditions were as nearly perfect as are ever apt to be achieved. All 3 days were perfectly clear and exposure meter readings were identical. Ground temperatures rose from 25° to 28°C between 10 A.M. and noon on April 2, while air temperatures rose from 21.5° to 24.5° during the same period. On April 3 ground temperatures rose from 22.5° to 27.5°, air temperatures from 22° to 24.5°. On April 4 ground temperatures rose from 23.5° to 28.5°, and air temperatures varied between 22° and 24°. The population studied is to some degree isolated, and the low vagility of the skinks has already been mentioned. These facts indicate that replacement following the removals of April 2 and 3 would be slight.

Although collecting efficiency was probably not as high along the south side of the field as along the north side during the first 5 samples, this would not influence the outcome of the removal experiment as long as the over-all efficiency was the same from one day to the next. During the collections on April 2, 3, and 4, records were made of the lizards observed which were not captured. These records served as indices of the relative efficiency with which lizards were captured. On the first day 21 lizards were captured on the north side, with 20 "misses." On the next day 11 were taken with 11 misses; on the last day 9 were taken with 14 misses. On the south side, for these 3 days, 11 were taken with 9 misses, 7 with 5 misses, and 7 with 7 misses. The totals for the north side were 41 captures and 45 misses, for the south side 25 captures and 21 misses. The observed proportions do not differ significantly from a hypothesized situation in which the collecting efficiency (50%) was the same for both edges of the field.

As nearly as is possible, then, the conditions of the removal method were fulfilled, the uncontrollable sources of error being differences in the activity of the lizards (despite apparently uniform conditions of light and temperature) and vagaries of sampling. Yet the population estimate (100) is much lower than the estimate obtained from capture-recapture data (175) and, indeed, less than the known number of lizards in the population. When removal began there were 72 marked lizards at risk. On April 2, 3, and 4, 21 marked and 45 unmarked were removed. We may assume that 51 marked animals had not been captured and were still at large, and this number, coupled with the 66 removed, indicates a minimal population size of 117. Again data from the north and south sides were analyzed separately. The north side population was estimated at 53 with a standard error of 7.5 (on the basis of removals of 21, 11, and 9 individuals). The south side populations was estimated at 43 with a standard error of 8.4 (on the basis of removals of 11, 7, and 7). The total (96) agrees with the total population estimate from the pooled data, suggesting that no unusual effect has been introduced by individuals from one side or the other. Zippin (*in litt.*) has observed that if marked lizards become wary and less susceptible to recapture, the capture-recapture analysis will over-estimate the population while if, during the removal program, the remaining animals become less susceptible to capture the removal estimate will be too low. Possibly the observed results are due, in part, to effects of this nature.

On the basis of this experiment, it is perhaps not justified to draw immutable conclusions as to the relative efficacy of the removal method and capture-recapture analysis. However, I have definite misgivings as to the advisability of estimating lizard populations on the basis of the removal of a relatively small number of individuals. It appears from other work that, at least as far as adult lizards are concerned, a marking and release program continued long enough will ultimately lead to a fairly accurate conception of the population size, even though the exact degree of reliability cannot be expressed quantitatively and will vary with the investigators involved. However, capture-recapture analysis would, in most cases, be the most efficient means of estimating the population. And there remains the problem of estimating numbers of juveniles. This is a recurrent theme in studies of *Sceloporus* populations (Fitch 1940, Stebbins 1944, Crenshaw 1955) and shows the need for the application of capture-recapture analysis. Relatively small fractions of the total numbers of such lizards are captured, even with prolonged effort. The numbers taken would usually be adequate to permit at least the use of the proportional index, but without such treatment they give an imperfect conception of the total numbers involved.

CONCLUSIONS

1. Marking of *Lygosoma* should be effected by cutting one toe from each foot. This procedure might be followed advantageously with other forms. It is not necessary to mark individually when the extent of activity ranges is already known, but a different mark should be used for each census.

2. The low vagility of little brown skinks minimizes the possibility of studying changes in population composition resulting from movements.

3. Individuals are equally at risk at all times of the day, *i.e.* there are no subpopulations utilizing the habitat at different times.

4. It is not possible to exclude effects due to increased wariness on the part of lizards which have been captured. There is also a possibility that lizards become less wary after capture and handling, though the removal estimate makes it appear unlikely that the population was underestimated from the recapture data.

5. Application of the removal method led to a patently low estimate. A removal program is always subject to invalidation owing to changes in weather and poses problems in standardizing the method and efficiency of capture.

6. Population estimates based on capture-recapture data require less time in the field than estimates obtained by marking virtually the entire population. Furthermore, it is likely that capture-recapture analysis will permit estimates (with indices of reliability) of numbers of 1st-year lizards.

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ON THE SOUTHERN LIMIT OF *BALANUS BALANOIDES* IN THE WESTERN ATLANTIC

Balanus balanoides (L.) is an abundant intertidal barnacle of boreo-arctic regions, found on both sides of the Atlantic and on northern Pacific coasts. Its distribution has aroused the interest of ecologists as an example of the effects of temperature on the geographical limits of species. Hutchins (1947) suggested that the southern limit of *B. balanoides* occurs where the mean winter sea surface temperature is approximately 8°C (46.4°F). The position of the 8° winter isotherm approximates the southern limits of this species on the American and European coasts of the Atlantic.

Recently, Barnes (1958) has discussed the world-wide distribution of *B. balanoides,* the factors limiting its distribution, and the mechanisms by which they might act. Records for *B. balanoides* along the middle Atlantic coast are indicated in Figure 1; each locality is referred to in the following report by number. Barnes found this species as far south as Sandy Hook, New Jersey (#1), on rocks, pilings, or other suitable substrates along the open coast. Although Darwin (1854) had reported this species from Delaware Bay (#5), Pilsbry (1916) did not find it south of Ocean City, New Jersey (#4). Leidy (1855) had found it at Atlantic City (#3), and Fowler (1912) had recorded it from Point Pleasant (#2). Although Ferguson and Jones (1949) had recorded *B. balanoides* from Hampton Roads, Virginia (#7), Barnes has suggested that this species was confused with *Balanus improvisus,* one of the common barnacles of that region, that was not recorded by Ferguson and Jones for the Norfolk peninsula. On the basis of these records, Barnes placed the southern limit of *B. balanoides* on this coast at 38°N latitude.

In the absence of more southerly records, Barnes found the attainment of low temperatures an inadequate explanation for the distribution. High summer temperatures and competition from other cirripedes were offered as alternative suggestions to account for the absence of this species south of New Jersey.

On the basis of observations and collections herein reported, it is unnecessary to invoke high summer temperatures or competition as an alternative explanation for the southern limit of *B. balanoides,* for its distribution extends south to a point where water temperature alone appears to be the critical factor.

Observations

On September 16, 1959, two of us (H.W.W., M.J.W.) collected in the vicinity of Ocean City, Maryland (#6). Large numbers of *Balanus balanoides* were found on rocks and concrete masonry on the point of West Ocean City which extends into Sinepuxent Bay opposite Ocean City Inlet. Here, *B. balanoides* was the only abundant barnacle. It was often restricted to locations where some sort of protection was offered, as in crevices, on the sides of rocks and underneath them, and about the basal attachment of *Fucus spiralis* on these rocks.

A more extensive population of *B. balanoides* was observed on the north side of Ocean City Inlet. Here, a jetty 800 yards long lies parallel to the inlet, extending into the ocean. At low tide, a typical intertidal zonation was apparent on the boulders that comprise the jetty. Uppermost was a zone of algae, primarily *Ulva lactuca* and *Enteromorpha* sp., next was a zone of very abundant and often crowded *Balanus balanoides,* and below that was a zone of *Mytilus edulis* which extended below the low tide level. On this jetty, *B. balanoides* is exposed to strong wave action and considerable water movement through the inlet.

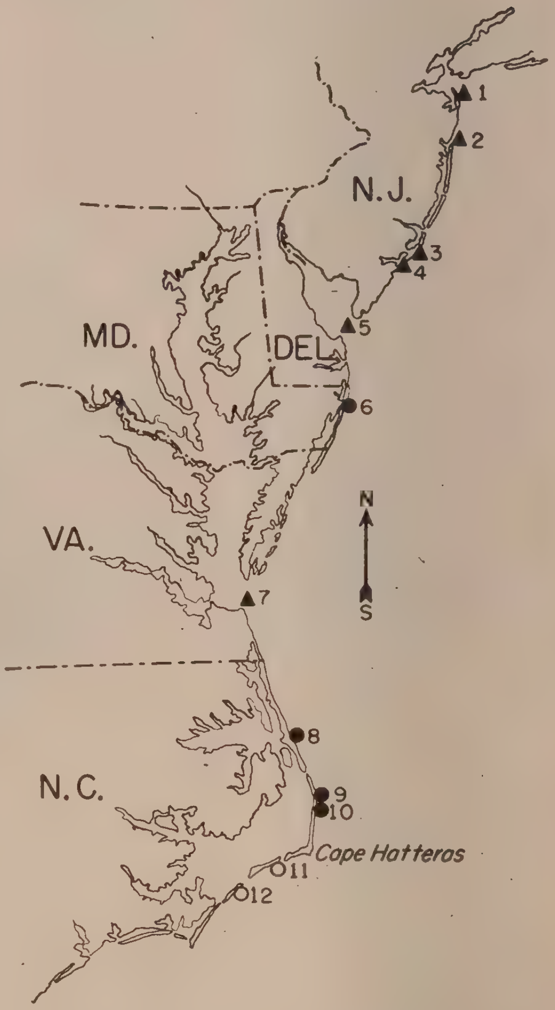

FIG. 1. Locality records for *Balanus balanoides* on the middle Atlantic coast. Solid triangles indicate previous records, solid circles indicate new records, and open circles indicate the absence of *B. balanoides.*

The occurrence of *Balanus balanoides* and of *Fucus spiralis* on the Maryland coast have not been reported previously; they are both intertidal organisms characteristic of New England rocky coasts. It seems unlikely that their appearance here is any indication of a change in local climate, but rather that the suitable substrates have become available for settlement only in recent times, specifically, since the opening of Ocean City Inlet in 1933.

In North Carolina, a study has been made of the fauna attached to several wrecks near the shoreline in the Cape Hatteras region. Five of these wrecks are of particular interest in discussing the distribution of *Balanus balanoides;* their positions are shown in Fig. 1. All but one of these wrecks ordinarily extend above the water surface; they are all metal wrecks and so provide a firm substrate for many sessile organisms. *Balanus balanoides* has been collected from wrecks at Kitty Hawk (#8), Rodanthe (#9), and Waves (#10). On the Rodanthe and Waves wrecks *B. balanoides* is the dominant animal in the zone lying above the *Mytilus edulis* zone. Specimens were also collected in the *Mytilus* zone, but the species always was restricted to an intertidal situation. On these wrecks, *Chthamalus fragilis, Balanus amphitrite,* and *B. improvisus* were also well represented, *C. fragilis* being particularly characteristic of the spray zone. Despite their presence, *B. balanoides* was abundant.

Balanus balanoides has not been found on wrecks off Ocracoke Island (#11) or off Portsmouth Island (#12), although many other organisms have been collected from their surfaces. Because the wreck off Ocracoke Island extends only 2 feet into the intertidal zone, the absence of *B. balanoides* might be attributed to scarcity of suitable substrate in intertidal regions. However, the wreck off Portsmouth Island extends well above mean low water and possesses an adequate representation of even spray zone organisms. If *B. balanoides* were living in the local area, it would be expected here.

Discussion

This occurrence of *Balanus balanoides* on the North Carolina coast moves the southern limit of its distribution several hundred miles southward to approximately 35°30′N latitude, a few miles north of Cape Hatteras. In view of this extension, there is no need to question the report by Ferguson and Jones (1949) of *B. balanoides* in the Hampton Roads area. The close approximation of this new limit to Cape Hatteras indicates that the factors responsible become critical at this point along the coast.

Hutchins' suggestion that the southern limit of this species coincides with the 8° winter isotherm deserves close attention. Parr (1933), Bumpus (1957), and Day (1958) have shown that there is a sharp break in winter water temperatures in the Cape Hatteras region. Their records indicate occasional winter water temperatures as low as 8°C at Diamond Shoals Lightship, 12 miles southeast of Cape Hatteras. Local hydrographic data show that surface water temperatures in mid-winter regularly drop below 8°C on beaches north of Cape Hatteras, while water temperatures south and west of the Cape remain above 10°C. Thus, the 8° isotherm fits perfectly the southern limit of *B. balanoides* on this coast.

Barnes (1958) regarded this 8° isotherm as only an empirical expression indicative of the barnacle's southern limit and did not consider this low water temperature to be essential to the completion of its life cycle. On the basis of his study of the effects of temperature on *B. balanoides* (Barnes 1959), he assumed that the limiting temperature factor was acting on the maturation and fertilization phases of the life cycle. He found that these processes took place at Woods Hole and Sandy Hook when water temperature was about 15°C. He concluded that a drop in air temperature is effective and essential in completing maturation and fertilization, that the required minimum air temperature is about 10°C, and that water temperature is only a useful indication of the requisite air temperature. At Hatteras, differences in winter air temperatures are unsatisfactory as an explanation for the presence of this species on wrecks north of the Cape and its absence from wrecks south of the Cape. The differences that occur in air temperatures at these 2 locations are primarily those induced by greater differences in water temperature.

Because records of *B. balanoides* did not extend as far south as "suitable" conditions of low air temperature, Barnes concluded that high summer air temperature and competition form an effective barrier to a more southward penetration on the coast. In regard to competition, the same species of barnacles, *Chthamalus fragilis, Balanus amphitrite,* and *B. improvisus,* were present on the southern wrecks as occurred on the northern wrecks where *B. balanoides* was very abundant. *Balanus eburneus* does not immediately take over the zone occupied by *B. balanoides* to the north as Barnes has suggested; in the Hatteras area, that species is found primarily in waters of lower salinity. There is no evidence that competition from other barnacles contributes to the limitation of *B. balanoides* in this area. Differences in summer air temperatures, like differences in winter air temperatures, appear to be inadequate to account for this limitation also.

Gradients found in water temperature at Cape Hatteras provide a more satisfactory explanation. In addition to the well-known winter-time temperature break in this area, documented by Parr, Bumpus, and Day, hydrographic studies in the area have shown that a sharp break in water temperature often occurs here in summer months (Wells and Gray 1960). Water temperatures at the wrecks north of the Cape and at the wrecks south of the Cape may show a summer-time difference of 5°C or more. Temperature gradients in this region are sufficient to produce a barrier at Cape Hatteras to the distribution of many organisms, and to explain the observed success and failure of *B. balanoides* over such a short distance.

Acknowledgments

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Summary

Collections of *Balanus balanoides* (L.) from Ocean City, Maryland, and at Kitty Hawk, Rodanthe, and Waves, North Carolina, have extended the southern limit for this species on the Atlantic coast to the region of Cape Hatteras. Factors responsible for the southern limitation of this species have been discussed. The suggestion is made that a sharp temperature break in the vicinity of Cape Hatteras is responsible for preventing farther southward extension of this species.

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AFTEREFFECTS OF LIGHT IN CHICKENS

Domestication of the fowl has been accompanied by selection for high egg number. Existing breeds of chickens represent a spectrum of populations which have attained varying stages of domestication as indicated by their rate of lay and related characteristics. Since one of the limiting factors of egg production in birds is photostimulation we were interested to learn how fowls of different genetic background would react to intermittent lighting regimes that have played no direct role during the domestication process.

Recent investigations of photostimulation of gonadal activity in birds have stressed the importance of the prior as well as the immediate light pattern on the nature of the response. Two noteworthy publications on this topic are Wolfson (1958) on sparrows, and Hutchinson and Taylor (1957) on domestic fowl. We have developed information on a similar problem, contrasting light regime with total lighting.

Beginning at 16 weeks of age, pullets were subjected to 2 successive light treatments. They had previously received normal daylight, supplemented during the first 8 weeks of brooding with low-intensity night lights. Then they were divided into 2 groups and placed in individual cages in 2 separate rooms with feed and water *ad libitum*. During phase 1 of the test (16 to 40 weeks of age) one group (D) was kept in complete darkness and the other group (I) received intermittent intense lighting for 1 minute each hour. Four 100-watt bulbs in the 30 x 30-foot room yielded an average of 4 foot-candles at cage level.

At 40 weeks of age, each of the above groups was randomly subdivided into 2 equal lots for phase 2 of the experiment. One lot in each chamber remained in place and the second groups were interchanged. At the same time, light regimes in the 2 chambers were changed—to continuous bright light in one and continuous dim light in the other. Continuous bright light was produced with the equipment used for intermittent lighting. Dim light was supplied by four 7.5-watt bulbs shielded by dark loosely woven saran; it barely permitted the reading of hand-written egg records on cages, and averaged 0.15 foot-candles at cage level. Phase 2 lasted from 40 to 50 weeks of age.

A control group of the WL x NH population (107 hens) was tested under normal daylight supplemented with artificial light to provide 14 continuous hours of light per day.

The lighting regimes were not entirely free of disturbance. The 2 rooms used were windowless and provided with forced ventilation, but were neither soundproofed nor insulated. Light traps were constructed at ventilators and entrances, but in bright day small amounts of light were visible from within. Photometric determination indicated that this light was less than 0.0002 foot-candles at the cage level. Small shielded pencil-flashlights, used in recording eggs once a day, were directed only at the mounted record cards. Room lighting was normal daylight through double doors on the day when the birds were moved and the pens cleaned at the start of phase 2. On 6 occasions when repair work was required in the darkened pens, flashlights were used.

The pullets used were of 3 different genetic origins:

1. Single Comb White Leghorns (WL) of a population selected for high egg production, referred to as the production line.
2. A 3rd-generation population (WL x A) from an outcross of the WL production line to an Araucana male of presumably unimproved origin.
3. The F_2 generation (WL x NH) of an outcross of the SCWL production line to a randomly selected line of New Hampshires.

The 3 types were assigned in proportionate numbers to the 4 possible treatment sequences. In the year that offspring were produced for this study, all 3 populations had been randomly propagated. Table I shows that the number of pullets available for the test at 16 weeks ranged from 25 Leghorns per treatment to about 51 of the WL x NH population.

RESULTS

At 16 weeks of age, when the birds were assigned to cages at random, four WL pullets had already begun to lay, and many birds showed signs of imminent sexual maturity. Most of the pullets, even when subjected to darkness and short intermittent lighting, came into pro-

TABLE I. Production characteristics of hens under light treatments of phase 1 and phase 2

Line	WL	WL	WLxA	WSxA	WLxNH	WLxNH	AVERAGE FOR PHASE 1 TREATMENT			WLxNH
Phase 1 Treatment*	D	I	D	I	D	I	D	I	Combined (D+I)	Control
Hens at 16 weeks of age (nos.)	25	25	37	35	47	51	—	—	—	107
Mortality 16-50 wks. (%)	28	12	24	26	21	14	24.3	17.3	20.8	4
Nonlayers (nos.)										
Phase 1 (16-40 wks.)	1	0	4	2	1	0	2	1	1.5	1
Phase 2 (40-50 wks.)	0	2	0	4	0	2	0	3	1.5	3
Age at First Egg (days)	175	154	202	168	167	161	181	161	171	156
Egg Production (%)										
Phase 1	44.4	54.3	35.6	43.4	52.8	62.6	44.3	53.4	48.9	72.1
Phase 2	57.0	31.4	48.9	29.6	57.6	39.9	54.5	33.6	44.1	55.3
Egg Weight at 40 wks. (gm)	54.3	56.5	53.4	55.8	60.2	58.7	56.0	57.0	56.5	58.6

* Phase 1 treatments (16-40 wks.): D: Continuous; I: One minute of bright light per hour.
Phase 2 treatment (40-50 wks.): Average of continuous bright and continuous dim light.

duction before 30 weeks of age. The WL x A population, presumed to be genetically least improved, had the highest incidence of non-layers, with 4 birds in complete darkness and 2 under intermittent lighting (Table I). These non-layers failed to lay during phase 1.

In 2 of the 3 populations, mortality during 16 to 40 weeks of age, as shown in Table I, was about twice as high in complete darkness as in intermittent lighting. In the WL x A cross, no difference was found between treatments. In the control group of the WL x NH population, tested under normal 14-hour light, mortality was found to be considerably lower than under either complete darkness of intermittent lighting.

The diurnal distribution of ovipositions during phase 1 was determined by recording eggs every 3 hours for 3 successive days when the hens were about 36 weeks old. About half of all eggs were laid between 3 A.M. and 7 A.M., and only about 3% between 11 A.M. and 7 P.M. A 24-hour rhythm of oviposition had undoubtedly been established in spite of what was intended to be light treatments lacking 24-hour periodicity. At least 4 sources of periodicity were, however, quite possibly operative under the conditions of this test. These were: Sound of daily activities on the premises, daily feeding and egg recording in pens, residual daylight, and daily temperature fluctuations (relatively pronounced in the latter part of the test).

The effectiveness of neural stimuli other than light in changing the diurnal rhythm of ovulation has been demonstrated by Fraps *et al.* (1947). They found that night feeding under continuous lighting could shift maximum egg-laying activity from day to night hours. It appears that the daily cycle of oviposition established in the present study was not primarily due to feeding, since the birds had feed before them at all times. Our results can be explained by a recent theory of Bastian and Zarrow (1955) according to which the onset of ovulation is regulated by the hen's daily activity. Since disturbances of daily chores ended each day at about 5 P.M., the birds of this experiment began their rest period perhaps 3 to 4 hours earlier than birds do under normal light regimes. Their laying activity was consequently advanced by that amount.

The effects on egg production of the 2 light treatments of phase 1 were consistent in all populations (Table I); Differences between dark and intermittent light treatments in sexual maturity varied considerably for the 3 lines. In the WL x A population, considered the most primitive genetically, the difference in average maturity was most pronounced; the relative effect of complete darkness on maturity was least in the WL x NH population which later had highest rate of lay.

In phase 2 of this study, the aftereffects of initial light treatments were measured under 2 regimes of continuing lighting (dim and bright). Percentage egg production for after-treaments shown in Table I is an average of the 2 regimes, whereas Table II gives more detailed analysis of the aftereffects of initial light treatment and of the direct effects of the 2nd continuous lighting regimes on eggs laid between 40 and 50 weeks of age. It may be noted that initial light treatments had more drastic effects on rate of lay in phase 2 than on immediate production. This is brought out by the analysis of variance shown in Table III, where the mean square due to first light treatment (804.91) exceeds that of the second treatment (35.43) more than twentyfold.

The 3 populations differed in their response to phase 2 treatment. In both WL and WL x NH populations, dim light produced appreciably less increase in production after dark treatment than did bright light, and greater reduction of egg numbers following intermittent light. For the WL x A population, on the other hand, there were small differences in egg numbers between dim and bright lighting of the 2nd period. Of the 3 populations, the highly selected WL production line appeared to be most sensitive to change in lighting regime. These genotype-environment interactions are reflected by a significant S x L interaction of Table III.

DISCUSSION

The study demonstrates that the response of domestic fowl to light depends on both the total amount of light energy (or intensity) supplied as well as the frequency of lighting periods. Egg production and sexual maturity observed in the first treatment period followed more or less anticipated patterns of response. Intermittent stimuli of bright light, even of the one-minute period employed, stimulated initiation and rate of ovulation considerably over those resulting from complete darkness. Since the Leghorns (WL) used in all populations had been under continued selection for egg number, it may not be

TABLE II. The aftereffects of intermittent lighting and dark-treatment (phase 1) on average egg number laid by survivors under (phase 2) continuous lighting for the period 40-50 weeks

LIGHTING TREATMENT		LINE OF BREEDING			Average of Combined Lines
Phase 1	Phase 2	SCWL	SCWLxA:F_2	NHxSCWL:F_2	
Dark	Bright	46.5	34.4	46.3	42.4
Dark	Dim	38.1	34.1	38.4	36.9
Dark	Average	42.3	34.2	42.4	39.6
Intermittent	Bright	25.2	18.1	28.5	22.6
Intermittent	Dim	17.6	23.0	27.2	23.9
Intermittent	Average	21.4	20.6	27.9	23.3
Average	Bright	35.8	26.2	37.4	33.2
Average	Dim	27.8	28.6	32.8	29.7
Overall Average........		31.8	27.4	35.1	31.4

TABLE III. Egg number of survivors during 40-50 weeks analysis of variance

Source of Variation	Degrees of Freedom	Mean Squares	Level of Significance
First Light Treatment F..........	1	804.91	0.03
Second Light Treatment S..........	1	35.43	0.06
F x S Interaction FS..........	1	13.15	0.20
Lines of Breeding L..........	2	59.83	0.04
F x L Interaction FL..........	2	15.74	0.20
S x L Interaction SL..........	2	27.75	0.06
F x S x L Interaction (Error).........	2	2.25	

surprising that they were able to maintain egg production even in the absence of light, as shown earlier in this laboratory by Wilson and Abpanalp (1956) and Wilson and Woodard (1958).

The effects of continuous light following dark treatment again closely follow what is already known on light response: a greater rate of lay following dark treatment when continuous light was given, and relatively better response for high intensity as contrasted to light of low intensity. These findings indicate that birds, preconditioned under constant suboptimal levels of lighting, will respond to subsequent increased amounts of light with higher egg production. The magnitude of response in egg production increases as the light intensity of aftertreatment is raised.

Although decreasing day length causes a reduction in egg production (Hutchinson and Taylor 1957, Sykes 1956), our results show that the same may happen with increasing total light energy when birds are subjected to pretreatment with intermittent light.

These results cannot be explained on the mere assumption of light-energy effects. In case of intermittent light followed by continuous lighting of equal intensity, the birds received about 60 times as much light energy per day for the second phase. Yet production dropped markedly. Loss of production was similar when dim light was used at a much lower intensity, with about double the daily light energy of preceding intermittent lighting. It is an open question whether this response is comparable to refractory behavior in wild birds. It should be noted that the least domesticated of the breeds used (WL x A) showed the smallest loss of production in phase 2.

We propose the explanation that intermittent lighting produces a high level of neural stimulation, after which continuous light, however intense, tends to be a let-down. Intermittent lighting produced a higher level of neural (or neurohormonal) stimulation than did continuous light of the same intensity. Switching to continuous light thus probably reduced gonadal activity in much the same way as decreasing daylength has classically been shown to do. We do not wish to imply that 1 minute of light per hour produces maximal stimulation, especially since intermittent light did not give maximum response in egg production. For maximum egg production, neural stimulation must then be given in conjuction with a small amount of light energy that serves to build up necessary levels of hormonal activity. In the case of the negative aftereffects of intermittent lighting observed here, one could then say that the neural mechanism necessary for effective action of available light had been rendered ineffective by preceding overstimulation.

Another tentative explanation for decreased egg production following intermittent lighting might be that birds under the latter condition were preconditioned to become active each time light was given. Continuous lighting would then tend to prevent hens from getting the necessary rest for efficient ovulatory activity. There does appear to be a difference in the "optimum" light regime for the development of refractoriness and for rate of production.

SUMMARY

The response of young pullets from 3 different genetic backgrounds to darkness and intermittent light followed by continuous light at high and low intensity was observed. The responses measured were: age at sexual maturity, egg production, egg weight and mortality.

The intermittent light treatment (one minute per hour) permitted the hens to lay at 53%, which was 10% higher than for hens kept in darkness. When the birds were subsequently given continuous light of high and low intensity, egg production was reduced noticeably in the group that had previously been exposed to intermittent lights. A significant interaction of light treatment and lines of breeding was observed.

A theoretical discussion of photostimulation is presented in an attempt to explain why continuous light may in some cases cause a reduction of egg production.

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THE MECHANISM EMPLOYED BY THE STARFISH, *ASTERIAS FORBESI* TO GAIN ACCESS TO THE INTERIOR OF THE BIVALVE, *VENUS MERCENARIA*[1]

INTRODUCTION

The mechanism employed by the starfish to gain access to the interior of bivalves has been a subject of research for many decades. Schiemenz (1895) postulated that the starfish opens clams through sheer force, while Delongschamps (1826), Parker (1881), van der Heyde (1922), Sawano and Mitsugi (1932), and Reese (1942) were led to the assumption that a toxic secretion, liberated by the starfish and introduced between the valves of the clam, was responsible for the opening. In recent years, 4 investigators, Burnett (1955), Feder (1955), Lavoie (1956) and Christensen (1957) have all demonstrated that starfish need not secrete any toxic substances between the valves, but are capable of pulling the valves apart employing forces of from 3000 to 5500 grams to overcome the resistance of the adductor muscles of the clam.

In 1955 I published a brief note summarizing the results of my experiments; however, several aspects of the feeding process which were observed were not described in any detail. Since none of the investigators mentioned above has given a complete account of the feeding process, it is hoped that this paper may contribute additional information regarding this baffling problem. All experiments mentioned in this paper were conducted during the summers of 1954 and 1955 at the Marine Biological Laboratory, Woods Hole, Massachusetts.

MATERIALS AND METHODS

The animals employed in this study were the common starfish, *Asterias forbesi* and the clam, *Venus mercenaria.* All experimental animals were collected at Woods Hole and kept in large tanks of running sea-water.

During feeding experiments, bivalves were simply dropped into a large wooden-bottomed tank containing several starved starfish. In order to obtain a specific resistance to opening, rubber bands were wrapped around the valves of several clams in which the adductor muscles had been severed. In order to determine whether an enzyme or a toxic substance was secreted between the valves, a small opening (1 mm in diameter) was filed in the edge of the valves of several clams to increase the flow of water into the mantle cavity. Other modifications, employed in feeding experiments, will be discussed in connection with "Observations."

OBSERVATIONS AND CONCLUSIONS

Eight clams, approximately 2½ inches in length, were wrapped with heavy cord in such a way that it was impossible to open the valves. These bound clams were then placed in an aquarium with a dozen starfish. If a starfish, in attempting to open such a bound clam, secreted some kind of a toxic substance between the valves, the clam should show a noticeable effect after the starfish had given up its feeding attempt.

All of the 8 clams were attacked within the next few days; the starfish remained in a humped position over the clams from 8 to 48 hours. The starfish were removed from the aquarium and the clams examined. In all instances the clams appeared to be unharmed. Their hearts were beating regularly, and their adductor muscles seemed to be perfectly intact. Since carmine particles, when introduced into the water containing the clams, failed to enter the mantle cavity, it was assumed that the clams possessed "hermetically sealed" valves.

However, the possibility existed that starfish might open the valves slightly through force, and then introduce a toxic substance between the valves. To test this hypothesis, a small V-shaped notch with an area of 1mm^2 was filed at the edges of the valves of 3 animals. The valves were tied shut as before and the animals placed in an aquarium containing a dozen starfish. It was found that all 3 of the starfish which attacked these animals were capable of passing their stomachs through the very small opening at the base of the notch. Hence, these clams were digested almost completely.

The above experiment was repeated with the following modifications. A small piece of shell, about one cm^2, was broken from the edges of the valves of several clams, and the opening thus formed was then covered with a fine bolting cloth (mesh size 40 microns). Since the bolting cloth possessed such a fine mesh, it presented a smooth surface upon which the tube feet of *Asterias* could make a firm attachment. Furthermore, the large opening in the valves allowed a great quantity of "clam-juice" to be liberated into the surrounding sea-water. If a clam, so prepared, was placed near a starfish, the starfish would quickly move to the clam and assume within a few minutes the humped position characteristic of feeding. In this way it was possible to have 4 or 5 starfish feeding at one time; it was also possible to determine the exact time of attack. The clams could now be removed at regular intervals and examined. The results of this experiment were as follows:

a) After 2 hours, 3 clams had suffered partial digestion of their mantles; the rest of the animal was intact in each case. One animal showed no digestion whatsoever at this time.

b) Three hours after attack one clam had undergone a

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[1] This paper is based upon a segment of a dissertation submitted to the faculty of Cornell University in partial fulfillment of the requirements for the degree of Master of Science. The author would like to express his deepest appreciation to Dr. John M. Anderson for his helpful suggestions and kind encouragement during the progress of this research, and for his excellent criticism during the preparation of the thesis from which this paper was derived.

complete digestion of one mantle and partial digestion of the other. No heart beat could be seen on this animal, but there may have been a temporary cessation because of the shock of opening the valves.

c) After 4 hours, 2 animals were examined. Both mantles on each specimen were nearly completely digested. The adductor muscles were still intact and the hearts still beating. Upon removal of one of the clams, the stomach of the starfish could be seen as a wide apron extended over the entire opening between the valves.

d) One animal examined after 5 hours had one mantle completely digested. The heart of this specimen was beating regularly.

e) After 20 hours, one animal had both mantles, gills, and part of the foot digested. This animal, of course, was dead at the time of examination.

f) After 24 hours, 2 clams were completely digested except for a part of the right adductor muscle and small bits of intestine and gonad.

Thus, there is strong evidence that *Asterias* secretes no poison before it begins to digest a clam. Since the starfish's stomach could not gain access to the mantle cavity, it was assumed that the digestive enzymes pass out through the mouth opening, and even after undergoing a great dilution in sea-water and "clam-juice," were still capable of literally digesting the clams alive.

Since it was conclusively shown that a starfish is capable of extending its stomach through a very small opening, and that the starfish possesses enzymes that are capable of digesting a living clam, it may be concluded that the starfish has only to open a clam's valves a millimeter or so in order to begin digestion.

The following experiment was carried out in order to determine whether a starfish is capable of opening a clam's valves through sheer force. A small notch was filed in the mid-ventral edges of the valves of several clams and the hook of a spring balance inserted in the opening. The amount of force necessary to produce a gape of about 2 millimeters was then recorded. Normally, a force of 7 to 10 pounds (3000-4500 gm), gradually applied, was sufficient to produce such a gape. The valves were then pried open with a steel probe and the adductor muscles severed. Strong rubber bands, sufficient to withstand a pull greater than that required to open the intact clam, were then wrapped around the valves. If the starfish succeeded in opening these bound clams, it would indicate that *Asterias* can open a quahog through force alone, since the rubber bands would not be subject to digestion or fatigue.

In 7 instances starfish were able to overcome the resistance of the rubber bands. A single observation of this process will be described in detail. After the starfish had oriented the bound clam (rubber band force 4500 grams), the tube feet at the ends of the arms appeared to be trying to move away from the clam. This could be a mechanism whereby a starfish exerts a pull. After 5 minutes the valves were opened about 2mm; they remained open for about 3 minutes and then snapped closed, presumably upon the everted stomach of the starfish, because of the pressure of the elastic bands. After a short time, however, the valves opened again, this time for 5 minutes. This process of alternate opening and closing continued for about a half hour. After this time it seemed that the starfish had oriented itself perfectly and was thus able to hold the valves open for as long as 10 minutes at a time. After 1½ hours the starfish gave up its feeding attempt and crawled away.

These results establish the fact that a starfish can open a clam through force alone; it is obviously unnecessary to postulate that a toxic substance is required in the process. Once the valves are open one mm or less, the enzyme introduced between the valves by the starfish, digests the clam while it is still living, hence causing a complete failure of the adductor muscles after a relatively short time.

SUMMARY

Numerous feeding experiments have demonstrated that *Asterias forbesi* can open the valves of *Venus mercenaria* through force alone. *Asterias* is capable of passing its stomach through a remarkably small opening in the valves. It then secretes powerful enzymes which bring about the digestion of the living tissues of the clam and ultimately result in the death of the animal. Previous reports that *Asterias* must secrete a poison in order to overcome the resistance of a clam's valves are not convincing in the light of present studies.

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STUDIES FROM THE AUTOTREPHON, V. A PAPER STRIP AS A RELATIVE HUMIDITY SENSING-ELEMENT

The Autotrephon, described in Stanley (1951) used a strand of human hair as a sensing element for the control of relative humidity. This strand was further discussed in Stanley (1953).

The hair strand, composed of 25 hairs each 12 in. long, was most difficult to make. The hairs were awkward to handle and unless all were at the same tension, they snapped and the strand rapidly broke down. One strand lasted 3 years, but the last one to be made broke across in a few hours. Furthermore, the hairs were somewhat stretchy, and made for uncertain contacts in the humidistat, resulting in as many as 50 brief contacts at "make" or "break."

Trial with paper strips, 12 in. long by 1¼ in. wide, using ordinary rather absorbent "Mimeograph" paper, has given excellent results. New clips were made up of duralumin as shown in Figure 1, having a stainless steel pin which threads through a loop in each end of the strip. The loop is made by folding over the end of the strip and sticking down with "Weldwood Contact Cement," but any good waterproof adhesive would do.

With hair strands, the wet bulb temperature oscillated with a period of a few minutes and an amplitude of about 0.15 to 0.20°C with numerous false contacts. With paper, the movement of the mercury column of a thermometer graduated in 1/10th degrees is too small to see even with a hand lens. At make or break, there is only one contact (or break of contact). Control does not wander, and stays steady for many days. As the paper strip is non-stretchy, adjustment to a given relative humidity is a little more difficult, as the movement of the adjusting nut is very small. Adjustment is however, more quickly done, because one does not have to adjust repeatedly until the stretch is removed.

It is possible that other papers might work better than Mimeograph paper, but the apparatus had to be in use, and as this paper was so completely successful, others were not tried.

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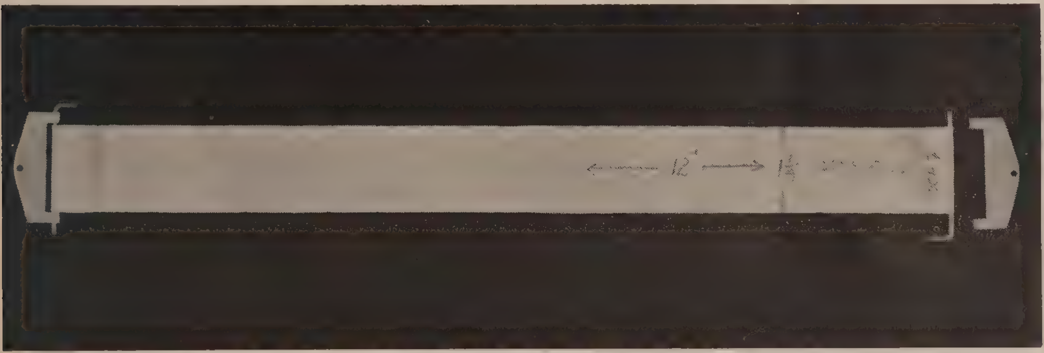

FIG. 1. Paper strip and end-clips, one of which is dis-assembled.

ON THE DIVERSITY OF THE COPEPOD POPULATION IN THE SARGASSO SEA OFF BERMUDA[1]

INTRODUCTION

Recent studies on the diversity of aquatic species relative to basic productivity and other environmental factors (*i.e.* Yount 1956) have aroused general interest in this aspect of population dynamics. It is thought that an application of this idea to marine zooplankton might be of value. The following paragraphs attempt to make some correlation of the diversity of the species of copepods with the standing crop of zooplankton and thus with the gross picture of basic productivity near Bermuda.

METHODS

Plankton samples were taken quantitatively (flow meter) with a No. 2 net (¾ meter) hauled obliquely from 500 meters to the surface at a station occupied regularly 15 miles S.E. of Bermuda. Preservation was made with neutralized formalin. The samples were cut with a plankton splitter to a convenient size; the copepods were separated out of the sub-sample and counted as to number and species. The index of population diversity used was taken from Fisher *et al.* (1943):

$$S = \alpha \log_e \left(1 + \frac{N}{\alpha}\right)$$

where: S = number of species in sample,

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[1] Contribution No. 270 from the Bermuda Biological Station. Work supported by Contract No. AT(30-1)-2078 with the Atomic Energy Commission.

α = index of diversity,
N = number of individuals in sample.

The diversity index, α, was extracted by the table presented in Fisher *et al.* (1943); a table of standard error for α in this paper was expanded graphically to obtain approximate standard errors.

Because of the relative ease of calculation, an attempt was made to utilize the diversity index presented by Margalef, 1959 (index of diversity $= \frac{S-1}{\log_e N}$, however as may be seen in Table I (but considering the limited number of counts) this index would seem not to possess the stability of the Fisher index at the levels of counts here found convenient. Because of this and the accessibility of the standard error in Fisher's tables, the latter index, α, is used throughout this discussion.

Table I. Counts of six subsamples from Atlantis cruise No. 178, haul No. 59 (see Table II)

Subsample	N	S	Div. index (Margalef)	α	Standard error α
A	113	16	3.27	5.14	0.84
A+B	259	21	3.61	5.50	0.74
A+B+C	375	23	3.72	5.38	0.62
A+B+C+D	478	24	3.74	5.52	0.56
A+B+C+D+E	591	25	3.77	5.38	0.54
A+B+C+D+E+F	749	27	3.94	5.44	0.46

In addition to plankton samples obtained near Bermuda, 3 samples from Atlantis cruise No. 178 in the tropical Atlantic were used for comparative purposes (see Table II). These tows were made near midnight with a No. 0, ¾ meter net towed at the surface for ½ hour at a speed of approximately 2 knots.

It should be emphasized that the 2 series consisting of Bermuda material and Atlantis cruise No. 178 cannot be compared directly because of the different nets used and because the former are oblique hauls (500 meters to surface) and the latter surface hauls.

Results

Quantities of copepods and species in the samples counted are given in Table II as well as total zooplankton volumes correlated with these samples and calculated values of diversity (α). Appropriate values of α are presented against the seasonal zooplankton volume picture of the Bermuda samples in Figure 1; it may be seen that for the available data the copepod population is more diverse (*i.e.* more species) during the periods of low standing crop or productivity. Conversely, during the spring bloom, α is significantly lower indicating a more homogeneous population. When corresponding values of α and zooplankton volumes are graphed on a semi-log basis (Figure 2) there is at least a high degree of correlation and some indication of a linear relationship. Here particularly, note the Atlantis cruise examples.

Discussion

Aside from the interesting inverse correlation between productivity and diversity (agreeing with Yount 1956 for fresh water diatoms), the data raise general questions concerning the diversity concept. It seems to be generally accepted that in northern regions there are fewer species with greater numbers of individuals than in more tropical areas. This is ordinarily attributed to "harsher" conditions (*i.e.* temperature) found in higher latitudes thus resulting in greater selectivity for a few well-adapted species. Latitude and temperature, however, may not necessarily be prime casual factors if one considers the comparisons in the Atlantis surface tows:

Haul	Location	Surface Temperature °C		α
3	29°37′N, 57°15′W	21.28	(30°16′N, 58°51′W)	8.0
261	15°23′N, 18°08′W	19.50	(15°14′N, 18°00′W)	3.8
59	13°04′N, 58°41′W	26.94	(13°03′N, 58°44′W)	5.4

In the Bermuda Samples during the spring phytoplankton blooms, food is certainly in maximum abundance which would allow a greater number of species to oc-

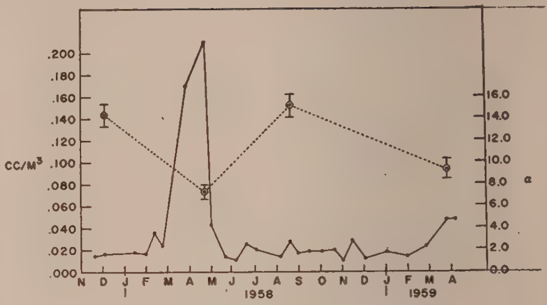

Fig. 1. Total zooplankton volume (solid line) and diversity index of copepods (broken line) in the Sargasso Sea off Bermuda. Standard error of the diversity index (α) is shown in each case.

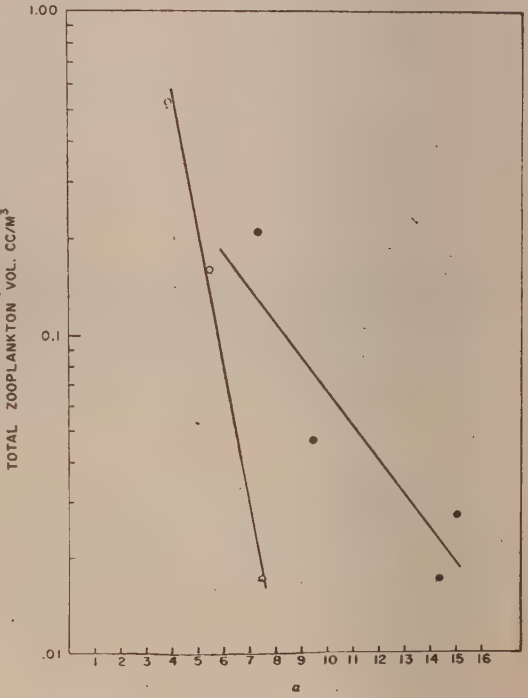

Fig. 2. The diversity index (α) of the copepods in the Bermuda area (filled circles) and in the tropical Atlantic from Atlantis #178 (open circles) as a function of total zooplankton volume.

TABLE II. Localities, dates, gross data and volumes of plankton samples

Locality	Date	Local Time	Vol. total zooplankton, cc/M³	No. (cop. counted)	S (Cop. spec. identified)	α	Standard error
15 m. SE of Bermuda. 500 m to surface	12/ 3/57	0430	0.017	910	60	14.4	1.1
"	4/21/58	1725	.021	861	35	7.3	0.6
"	8/18/58	1045	0.027	1109	65	15.1	1.1
"	3/25/59	1600	0.047	716	41	9.4	0.9
Atlantis #178 29°37′N 57°15′W Haul #3	1/25/52	night	0.017	723	34	7.4	0.7
15°23′N 18°08′W Haul #261	2/20/52	night	0.53	1665	23	3.8	<0.4
13°03′N 58°44′W Haul #59	3/ 9/52	night	0.16	749	27	5.4	0.5

cur (Menzel and Ryther 1959). Conversely, during times of low productivity, when the phytoplankton is sparse, one would expect only a few hardy or efficient species to survive. This does not seem to be the case. Certainly, a different type of population in not involved, for most of the species bulking large in times of bloom are also represented in times of low productivity. It would seem possible, then, that the values of α given, occur in a considerable variety of environmental conditions with little in common except the magnitude of the complex here described as standing crop.

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ANTS, ACACIAS AND BROWSING MAMMALS

INTRODUCTION

Almost any plant with hollow or pithy stems, twigs, thorns or other preformed cavities can serve as shelter for a nest of ants, and in most temperate and tropical countries many kinds of ants take advantage of such sites. The occupancy of plant cavities may be an irregular or occasional thing for some ants, but for other kinds it is obligatory. And on the side of the plants, we find that some kinds occasionally harbor ants, others frequently do, and some are almost never without.

In quite a few extreme cases, the plants have developed what appear to be special accommodations for the ants that inhabit them. The trees of the moraceous genus *Cecropia,* for instance, have hollow internodes partitioned by thin septa, and at the axils are pits or grooves at weak places in the wall through which ants can easily gnaw to gain access from the outside. Some plants, for example the *Tococa* of the American tropics, bear at their leaf bases twin pouches often serving as domatia for ants. Members of the genus *Acacia,* both in the New World and the Old, bear special inflated stipular spines that are regularly inhabited by ants, including some species that have never been found living anywhere else but in these particular domiciles.

Plants that bear such regularly ant-adapted domatia are called myrmecophytes. In addition to the provisions for shelter, myrmecophytes usually carry extrafloral nectaries, leaf surface "pearl glands," Beltian bodies, trichilia or other organs furnishing concentrated sugary, fatty or proteinaceous matter utilized as food by the guest ants (see Figure 1). Extrafloral nectaries or glands producing nutritious substances are by no means restricted to true myrmecophytes, but are found in many plant families, particularly among the angiosperms. The function of these nectaries and glands, found usually on the leaves, has been disputed for a long time, and cannot yet be considered as established. But we do know that many of these organs are visited by ants and other insects, particularly aculeate Hymenoptera, during some seasons.

During the last hundred years and more, many leading biologists, including Darwin, have been interested in ant plants and extrafloral nectaries. To oversimplify, we may consider all observers to belong to either of 2 schools of thought. The first or "protectionist" school believes that

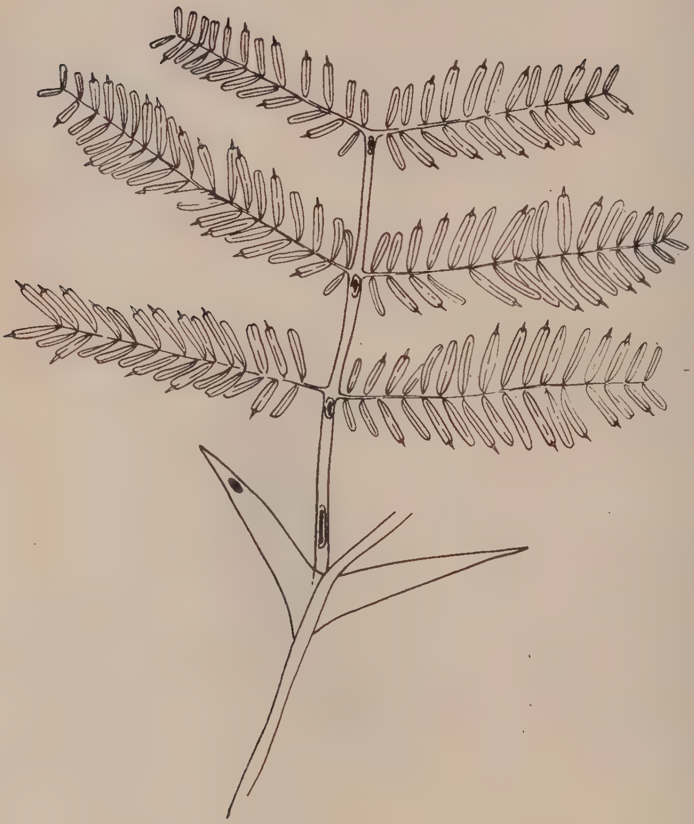

FIG. 1. *Acacia cornigera* L., showing a complete leaf with its stipular spines and a portion of the twig to which it is attached. Note Beltian bodies at the tips of many leaflets, and elongate crateriform glands or nectaries on petiole and rhachis. The hole near the tip of the spine was made for entrance by an ant of the *Pseudomyrmex belti* complex. Natural size.

the ant plants, as well as many plants with just the extrafloral nectaries or glands, receive the benefit of protection from the ants (and other insects, particularly stinging bees and wasps) that they attract or harbor. Thomas Belt, author of "A Naturalist in Nicaragua" (1874) was early prominent in this school. The 2nd or "exploitationist" school, of which W. M. Wheeler was the present century's most tireless exponent, denies that the plants receive significant benefit from the presence of ants or other aculeate Hymenoptera, and claims that these insects merely take a mildly parasitic advantage of features of the plant that happen to attract them.

The protectionist argument, as exemplified by Belt's discussion of Nicaragua ant acacias occupied by *Pseudomyrmex* and other ants, points to the striking modifications of the plant that provide food (Beltian bodies, foliar nectaries) and shelter ("bull's-horn" thorn domatia) for the ants. These features are considered to be adaptations that help to protect the plant against mammals and insects that would otherwise feed on the foliage.

The exploitationists, particularly Wheeler (1913, 1942), answer by listing many species of insects found damaging the foliage of acacias and other ant plants despite their occupancy by ants. As for browsing mammals, Wheeler thinks that "it must be evident at once, to anyone who sees these plants growing in the savannahs of Panama and Guatemala, that their thorns alone would protect them from the attacks of horses and cattle. . . ."

On the face of it, Belt's opinion has long seemed to me more attractive than that of the exploitationists. We cannot expect any protective adaptation to be absolutely effective; the real question is whether it is effective enough to confer a significant selective advantage on the plants that have it. Wheeler's reference to the thorns as sufficient protection against horses and cows is beside the point, for there are and have been many other ungulates that regularly browse in formidably thorny foliage. After all, the buccal adaptations of animals like camels and goats may be evolutionary response to the very fact of thorniness. Then there remains the question, concerning the often elaborate modifications of the plants, of just what other selective pressures conceivably could have produced them.

It may eventually be possible for someone with the time and resources to test the adaptive value of the ants to the ant plants through feeding-choice experiments with goats or other browsers. Until such time as these experiments are performed, however, we shall have to judge the issue on less direct evidence. A broad look at the genus *Acacia* provides some suggestive data.

The Genus Acacia

The genus *Acacia* is a very widespread, chiefly tropical and subtropical assemblage of more than 700 species of leguminous trees and shrubs belonging to a group which includes *Mimosa, Pithecolobium*, and *Inga.* Most of the species live where the rainfall is low or markedly seasonal, and many show various degrees of xerophytic adaptation. It does not follow from this that the genus originated in arid or semiarid regions (as some botanists believe), because most of the xerophytic features are clearly secondary within the genus. This is especially true in Australia, which has the lion's share of the xerophytic types, and which also has a number of more generalized species living in wet forest (Andrews 1915).

Acacia is an old genus, reaching at least quite far back into the Tertiary. Primitively, the genus appears to have had the pinnately compound leaves of its sister genera in the Leguminosae, and it doubtless also had the stipular spines that have persisted in many of its species to the present. In a large number of the species, though, the leaves have been reduced to needle-, scale-, or strap-like remnants called *phyllodia,* representing the modified petiole of the original leaf. Such reduction is especially characteristic of most of the numerous Australian species commonly called "wattle" and "mulga" (Figure 2). These xerophytes in Australia have, as a rule, also lost the stipular spines—a most interesting evolutionary development.

There has been no comprehensive review of the genus since that of Bentham (1876), and revision of some components is long overdue. I have taken information on *Acacia* from Andrews (1915) and Atchison (1949), as well as from von Mueller (1887-1888) on Australian acacias, and Wheeler (1942) on the American myrmecophytic forms.

The six sections of Bentham's classification of *Acacia* are: Phyllodineae (*ca.* 400 species, chiefly Australian); Botryocephalae (12 species in eastern Australia); Pulchellae (about 10 species in Western Australia); Filicinae (2 or 3 species in the Caribbean area); Vulgares (perhaps 100 species, primarily New World); Gummiferae (about 200 species, mainly in Africa, Asia and the Americas, with a few species reaching northern Australia).

It can be seen from the above that Australia contains not only a majority of the species, but that it also supports the greatest phyletic diversity in the genus. Yet it is not in Australia, but in the much less diverse African and neotropical *Acacia* floras that the true myrmecophytes have arisen twice and possibly even 3 times independently. Australia has no known myrmecophytic acacias. This is certainly not due to any scarcity of ants, for the Australian fauna is one of the richest in species and individual ants of any of the continental areas.

Enormous tracts of arid inland Australia are dominated by species of *Acacia,* mainly in the form of small trees, among which *A. aneura* (mulga), *A. harpophylla* (brigalow), *A. Sowdenii* (myall), *A. pendula* (boree), *A. acuminata* (jam) and *A. Cambagei* (gidgee) are best known. In addition to their lack of myrmecophytic adaptations, there is something else interesting about these trees: they have no spines. The fact that Australian savannah and desert tree-acacias (as well as most associated *Casuarina,* eucalypts, etc.) are unarmed is even more interesting when one considers their ecological equivalents in other parts of the world—say, in east Africa or Mexico, where the dominant small trees of the open country are predominantly thorny, and often formidably so. When I traveled through inland Australia in 1950 and 1951, I was very much surprised at the unarmed nature of the trees and larger shrubs I saw there. True, spiny plants abounded among the lower vegetation; the well-known spiny grasses *Triodia* and *Spinifex,* especially the first, were almost the only plants to be seen over vast reaches of the driest country. Also, according to Mr. J. H. Willis of the National Herbarium of Victoria (*in litt.*), some of the acacias of Australia are highly spinescent, but in arid open areas such species are mostly small shrubs, such as *A. spinescens, A. colletioides, A. acanthoclada* and *A. ferocior.* Other spiny species, *e.g., A. oxycedrus, A. pulchella* and *A. verticillata,* form dense scrubs in better-watered forest country.

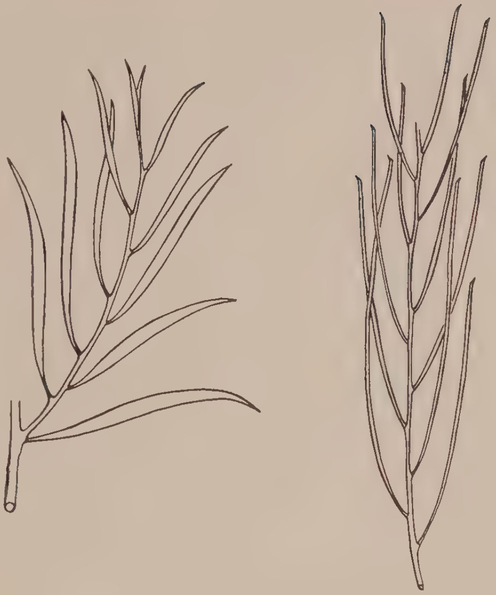

Fig. 2. Two leafy twigs of *Acacia aneura* F. v M., the Australian mulga tree, showing different forms of phyllodes in this species. Adapted from von Mueller, 1887-1888. One half natural size.

In *Acacia,* the apparent primitive condition is the presence of spiniform stipules. It is interesting, as noted above, that most of the Australian acacias have lost the stipules altogether. In the armed Australian members of the genus, the armament has arisen secondarily in various ways, through the modification of phyllodes, branchlets, or even peduncles. This suggests that *Acacia* in Australia passed through an earlier period in which spininess had little adaptive value, followed by a time in which selective pressures again arose favoring the development of spines *de novo* in shrubs of the forested country and in the lower shrubs of the open country.

Unfortunately, we have no observations bearing on the possible function of such phyllodial "glands" as have been rather meagerly reported for Australian acacias. Indications are that foliar nectaries are poorly developed, or that they are even absent, in most Australian species. In fact, extrafloral nectaries seem much rarer on Australian plants than on those of other countries, though this point requires checking. That this is not due to any differences in the ants is indicated by the observations I made on *Chrysanthemoides monilifera,* a composite shrub from South Africa now widely escaped in and around Melbourne, where it is conspicuous chiefly on account of the extraordinary numbers of ants, mutillids, thynnid wasps and other aculeate Hymenoptera it attracts. Although this plant bore no conspicuous nectaries on its foliage, I was able to determine with the help of Miss Maisie Fawcett and graduate students of the Botany Department at the University of Melbourne that the Hymenoptera were being drawn by a sugary substance secreted by microscopic unicellular glands in its leaf surface (unpublished notes). Native acacias, eucalypts and ti-trees growing next to these plants attracted no such aggregations of insects to their leaves.

Mr. J. H. Willis (*in litt.*) calls attention to the fact that only 2 genera of true myrmecophytes, the "ant bulb" epiphytes *Myrmecodia* and *Hydnophytum,* are known from Australia, but these are special cases. Both of these small plants belong to the Indo-Melanesian flora, like most of the rain forest trees of northeastern Australia upon which they grow. (The adaptive relationship of the ants that live in these plants to the plants themselves has never been clarified, but it has been suggested that the excreted waste of the ants may somehow be utilized as nutriment by the plant.)

Discussion and Conclusions

It seems from all this that spininess and attractiveness to ants (and other aculeates), including true myrmecophytism, may be at least roughly correlated geographically, and we can therefore consider the possibility that they are adaptively related. What then are the selective forces that may have induced these adaptations? We have seen already that aridity by itself is an unlikely influence. Phytophagous insects are not likely to be involved in the evolution of spines, though they could have influenced myrmecophytic adaptation (and may possibly have in some cases). This brings us to the browsing mammals—one of Belt's original suggestions, and the one influence I know of that fits all of the facts available. (Keller 1892, and other writers have backed the browsing-mammal theory of myrmecophytism in *Acacia;* for references see Paoli 1930: 173). Large, tree-browsing herbivores are now or recently have been abundant in Africa and tropical America in the same general areas where spiny and myrmecophytic acacias now occur. In Africa, at least, the acacias constitute one of the chief food sources for many browsing mammals. In Australia, on the contrary, no such radiation of large browsers seems to have taken place.

The endemic Australian mammal fauna is limited to marsupials, monotremes, rodents and bats. Of these, the kangaroo (*Macropus*) is the largest survivor. The kangaroos, despite their habitus, are chiefly grazers. Larger fossil marsupials existed in the Pliocene and Pleistocene, before which we have no record. The large Pliocene-Pleistocene mammals, all now extinct, were giant kangaroos (presumably grazers like *Macropus*), and some ponderous marsupial herbivores, exemplified by *Diprotodon* and *Nototherium.* The last 2 genera (one of which survived until about 10,000 years ago and was probably finally wiped out by the early aborigines) were perhaps the closest things to "ungulate life-forms" ever produced by the marsupials anywhere, but even they seem not to have gone very far toward the ungulate adaptive zone. We do not know how *Nototherium* and *Diprotodon* fed, or what they fed upon, but even if they were browsers to some extent, it seems reasonably clear that they never added up to a powerful browsing fauna having the magnitude and effect of the present and Tertiary ungulates and ungulate-like animals in other parts of the world. The lack of spines and myrmecophytic adaptations in the open-country tree acacias of Australia has resulted, in my opinion, from the long-continued absence or scarcity of effective large browsers. That many of the smaller shrubby acacias and spiny grasses, as well as shrubs of the closed forest, have developed spininess is understandable when one considers that the kangaroos, smaller marsupials and rodents do feed upon them.

There is one more interesting point in this connection. Wilson (1959) has already pointed out that the Melanesian ant faunas (particularly that of New Caledonia) are relatively deficient in arboreal species that nest in hollow twigs in place on the trees and shrubs. I think the same is more or less true of the Australian ant fauna. By contrast, the other temperate and tropical continental faunas are rich in twig- and stem-dwelling ant species. I think this situation may reflect an actual relative shortage of hollow-twig habitats in the Australian-Melanesian area, and this shortage could in turn imply the selective advantage to plants of twig-hollowness in countries where both browsing and arboreal leaf-eating mammal faunas are better developed.

There is unanimous agreement that the fiercely stinging *Pseudomyrmex* ants of the American tropics are very aggressive and effectively unpleasant against human disturbers of their foliage; they make the tree they inhabit a sort of super-nettle. They must represent at least a deterrent annoyance to would-be browsing mammals. The *Crematogaster* found in both neotropical and east African acacias are also very aggressive, swarming upon the observer when he disturbs the foliage and sinking their jaws into his skin. The effectiveness of this behavior has been disputed, probably because different observers have experienced the attacks of different species with varied aggressive talent. Paoli found the bites of some acacia-dwelling species only mildly irritating on the skin of his arm. Other observers have found the experience more unpleasant; I myself very much dislike the massed attack of most *Crematogaster* species against my hands and arms. However this may be, it must be remembered that a browsing camel or giraffe is not putting its limbs into the foliage, but is presenting its head with all the presumably vulnerable tissues connected with the eyes, nose, mouth and ears. True, these areas are frequently protected by one means or another.

The nictitating membrane of the eye is one obvious protection present in browsers (although a thorough survey study of its occurrence and its function seems never to have been made). The nictitans is present, although rudimentary, in several carnivores, but is strongly developed in many of the animals that feed on ants and termites, such as the aardvark (*Orycteropus*) and scaly anteaters (*Manis*); mammals such as the armadillos, aardvarks and echidnas have keratinized corneal epithelia, and some of them can close their nostrils and even their ear openings. Ungulates all possess a nictitans, but it is very variously developed in different species (Walls 1942); comparisons are difficult from the scattered and often incomplete descriptions in the literature. Camels are well known to have a good nictitans and tough, leathery mouth linings that permit them to feed on most thorny vegetation with reasonable ease, and there is now good reason, I believe, to consider the possibility

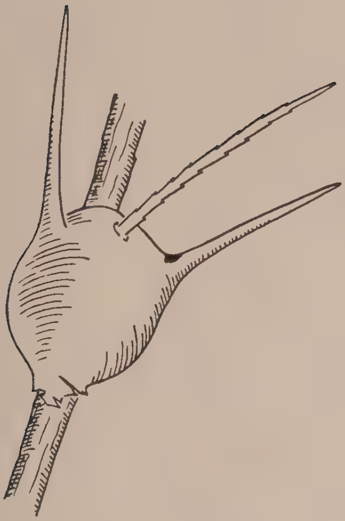

FIG. 3. Stipular spines of *Acacia pseudofistula* Harms, showing their bases swollen into a single globular domatium with the entrance to a *Crematogaster* nest chamber on the right. The rhachis, dry and denuded of leaflets, is the serrate piece projecting from the top of the domatium. Natural size.

that the camel's nictitans is more than just a screen against sandstorms.

I believe, with Belt, that the myrmecophytic adaptations of *Acacia* are adaptive for the plant in that they encourage the presence of ants, and that the ants serve a function similar to that of spines and prickles in preventing or deterring to some extent the browsing of herbivorous mammals. Neither the ants nor the spines, nor both together, should be expected to provide absolute protection for the plant. As the plants developed their protection, the animals also had to counter-adapt or lose to competition in the selective race. The evidence seems to show that, where effective browsing mammal faunas are now or recently have been present, the ants have paid their keep. The myrmecophytic adaptations and extrafloral nectaries of the plants ought to be no more mysterious in their function than are the spines or poisonous foliage of many plants. (One wonders whether the peculiar high, flat-topped crown shape of some of the African acacias is not also an adaptive response to browsing).

Finally, it should be stated that, although the circumstances suggest in the case of *Acacia* that browsing mammals may be the chief selective agent favoring myrmecophytism, I am by no means depreciating phytophagous insects as another factor. In acacias, and even more so in some other myrmecophytic plants, it is possible that the guest ant species may serve to protect the host plant from insect attack to some extent, no matter how much insect damage may be noted by an observer in actual cases. Protection by ants against defoliating leaf beetles is definitely indicated for the tropical boraginaceous shrub *Cordia macrostachya* (Simmonds 1949), which belongs to a genus otherwise notable for its myrmecophytic species. Besides ants, of course, plants may attract other kinds of insects that have a potentially beneficial effect. Townes (1958) emphasizes the attractiveness (if not the necessity) of foliar nectaries to many kinds of ichneumon wasps, some of which "spend several hours a day working over the foliage of trees and shrubs with small nectaries." Since ichneumonids are primary foes of phytophagous moth, beetle and sawfly larvae, the possibility of effective mutualism between wasp and plant must also be considered here. The whole subject of extrafloral nectaries is in fact wide open to the careful study it has so long required.

SUMMARY

1. Many plants (myrmecophytes) bear special structures suited to the housing of ants, and are regularly inhabited by them. Most myrmecophytes, and many other plants as well, are furnished with foliar nectaries or other food bodies that are exploited by ants and other insects.

2. Of the 2 schools that have argued the adaptive significance of these modifications, the protectionist school claims that the ants and other insects attracted to these plants do benefit from the plant, and some of them in return afford it some measure of protection from herbivorous mammalian and insect enemies. The exploitationist school holds that the insects benefit from the products of the plant without conferring any significant advantage upon the plant in return.

3. Trees and shrubs of the genus *Acacia*, which contains some of the classic myrmecophytic species, show pecularities in the geographical distribution of certain characters that may have a bearing upon the question of myrmecophytic adaptation. The primarily Australian sections of the genus, at least the arborescent open-country species, lack myrmecophytic structures, have mostly lost their spiniform stipules, and have no conspicuous system of extrafloral nectaries. The Afro-Asian and tropical American *Acacia* are mostly very spiny, and strongly myrmecophytic groups have arisen in both hemispheres independently.

4. This distribution is in agreement with the known occurrence, in the recent geological past and the present, of large and effective faunas of browsing mammals. It is therefore suggested that the presence or absence of spininess, myrmecophytism, and some types of nectaries may be an adaptive response of the plants to the presence of such mammal faunas.

5. The claims of the protectionist school for the adaptive nature of some kinds of extrafloral nectaries and ant domiciles in attracting insect "guards" against phytophagous insects also seem reasonable, but proper study of the problem has scarcely begun.

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JUVENILE PENAEID SHRIMP IN THE SHALLOW GULF OF MEXICO[1]

Many authors have commented on the absence of juvenile shrimp of the genus *Penaeus* in the shallow Gulf of Mexico (Weymouth, Lindner, and Anderson 1933, Gunter 1950, and others). This absence has given rise to the presumption that the postlarvae must reach the bays or die. The predominance of juveniles in shallow, low-salinity estuaries is very well known. Previous workers found juveniles almost exclusively in low salinities and there has been argument as to whether this was a relationship to salinity *per se*. However, Lindner and Anderson (1956) found that size of young shrimp correlated more with locality than with salinity and they concluded that salinity over broad ranges was not important although it might be an important stimulus to migration. Hildebrand (1955) noted that *P. duorarum* is found predominately on sandier substrates, while *P. aztecus* and *P. setiferus* seem to prefer muds. He gave no data on salinity but found juvenile *P. duorarum* in high salinities in "grass" flats.

Collections of juvenile shrimp in East Texas have given some insight into the distribution of juvenile penaeids as related to certain environmental factors. On September 28, 1958, numerous juvenile *Penaeus setiferus* (L.) were taken with a small seine in the surf at Gilchrist, Texas. This area has been pictured and described by Reid (1955, 1956). Sensing that this was perhaps an unusual occurrence of these small shrimp, on October 6 we collected along the beach from Sabine Pass to Bolivar Roads, seining at 10 mile intervals. Seining twice with a 10-foot minnow seine at each stop, from 58 to 218 *P. setiferus* from 20 to 83 mm rostrum-telson length were taken; most between the lengths of 30 to 60 mm. A total of 628 was taken at the 6 stops or a mean of 52.3 per haul. On October 16 two places between Gilchrist and the Bolivar Jetty yielded more than 500 *P. setiferus* juveniles. On November 6, a few juveniles were found near Gilchrist, but none was found thereafter in the surf through May 20, 1959, although we visited the beach in this area once a month. The disappearance of *P. setiferus* from the beach coincided with rapid emigration from the bays.

Postlarval penaeids were taken in plankton nets, but their identity is uncertain. Only one other penaeid, *Xiphopenaeus krøyeri* (Heller), was taken with *P. setiferus*, but it was uncommon.

On May 8, 1959, a single juvenile of *Penaeus aztecus* (Ives), 31 mm, was taken from the surf about 10 miles northeast of Gilchrist. The specimen may have come from a bed of clay off the beach in about 3 feet of water.

Northeast of Gilchrist in the Chenier plain region are numerous outcroppings of clay bottom in the surf zone. However, most of the bottom was sand, sometimes over clay. All of the bottom southwest of Gilchrist was sand. Salinities where shrimp were taken were from 22.2 to 26.5 °/oo and water temperatures from 19.7 to 26.4°C. A strong alongshore current to the southwest was observed whenever we were on the beach. The surf was usually rough, and consequently turbid.

Juvenile penaeids are known from 2 other relatively high salinity localities in the area. The Intracoastal Waterway where it runs north of West Bay, an arm of Galveston Bay, contained numerous *P. setiferus* juveniles in the fall of 1958 and numerous *P. aztecus* juveniles in the spring of 1959. These populations were similar in size to populations of shrimp found elsewhere in the bays only in lower salinites in the upper parts of the bays. The channel is artificial, with a depth of 12 feet and a hard clay bottom. The bottom was consistently covered with dense growths of red algae, some of which was identified by Dr. J. T. Conover as *Gracilaria cornea.* Salinities in this area were about 19 to 26 °/oo when shrimp were found. Adjacent areas in West Bay with similar salinities never contained juveniles, but the *Spartina* marsh to the north was not sampled. Bait shrimpers tell me that small shrimp are found there every year, indicating a yearly recurrence of juveniles in this relatively high salinity locality.

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[1] Contribution no. 51 from the Marine Laboratory, Texas Game and Fish Commission, Rockport, Texas. Collections were aided by W. C. Renfro and J. K. Shidler.

Juvenile *Penaeus duorarum* Burkenroad are known only from "grass" flats of predominately *Thalassia testudinum* in West Bay near San Luis Pass. *P. duorarum* is euryhaline so the absence of juveniles from low salinities in the area may be due to the absence of grassy areas.

It would seem that within certain areas, at least, salinity in broad ranges is inconsequential to young shrimp. All of the habitats where juveniles have been found could offer protection from predators. Low salinity presumably slows predation, as does a rolling, turbid surf and areas with large expanses of vegetation. The occurrence of juvenile *P. setiferus* on an outer beach is apparently rare. The population may have been transient and temporary, but it existed in the surf zone for about the same period that juvenile *P. setiferus* were abundant in the low salinity estuaries. It appears that juvenile *P. setiferus* and *P. aztecus* can populate areas of relatively high salinity if other environmental factors are ideal.

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FISHES AND THEIR PARASITE-MIX AS OBJECTS FOR ECOLOGICAL STUDIES

All studies of parasites with their hosts are studies in ecology because each member of the associating pair is a part of the environment of the other member. When a parasite is studied by itself, separated from its environment, only a part, and often a small part, of its total biology can be understood. The modern approach to parasitology envisages an ecological complex formed by the parasite, the vector, the host and various features of the host's environment. The total parasite fauna and flora of an animal or plant can conveniently be termed the "parasite-mix." Fishes, next to man, have been most widely explored for their parasites, and since fishes are commonly involved in ecological investigations, a presentation to ecologists of parasitological problems relating to fishes and all of their parasites should be of value in enlarging the range of hydrobiological investigations.

The gills of fishes, in spite of free communication with surrounding waters, constitute a fascinating host habitat with a circumscribed assemblance of parasites most of which present an aspect of intimate fellowship. A few members of the assemblage, however (such as certain flagellates and nematodes), refuse to respect the ill-defined ecological barriers of the hostal habitat. Among the gill filaments of one fish, particularly a freshwater species, there may be crowded together, either on or just under the surface of the filaments, *Trichodina* (a ciliate), monogenetic trematodes, copepods, leeches, metacercarial cysts, myxosporidian cysts, as well as fungal and bacterial parasites. Other forms to be found on fish gills include isopods, tapeworm cysts and various protozoa. Many of the gill parasites may also be found on or in the skin where protozoal species such as *Costia* (a flagellate) and *Ichthyopthirius* (a ciliate) often cause considerable damage or even death to the host.

The same general comments as those made for gills can be made for the intestine. Tapeworms, trematodes, acanthocephalans, nematodes, protozoa, bacteria and fungi all thrive in the ever-changing fluids of the fish digestive tract. Other organs may be crowded with coccidia, microsporidia, myxosporidia and nematodes. The blood may carry flagellates, sporozoa or larval nematodes.

It has been truly said that the ideal host is tolerant and long suffering. But the word "suffer" is, of course, anthropocentric, and the fishes so loaded with parasites usually exhibit little or no evidence of being incapacitated or even "troubled" by their uninvited guests. The apparent tolerance of the host, however, is quietly deceiving. Little imagination is required to recognize the continuous ferment of activity that must take place if both the parasites and their host are to survive. Competition for space and for food (which is often the blood or tissues of the host) are of prime importance. But imagination is not enough. Most of the distressingly intricate relationships between parasites and their hosts are mysteries whose depths remain unplumbed, but the physiologist and biochemist are making headway by providing new insights into enzymatic and other relationships between host and parasite—relationships that profoundly affect both partners.

The General Environment of the Parasite

Compilations of fish parasites have often been made, but such lists usually are based upon summer collections because the investigator is often a college professor who can find the necessary time to do the work only during vacation months. Similar collections during the winter months usually disclose not only smaller numbers of some of the parasite species, but a different ratio of numbers. The food of fishes, especially as it relates to intermediate hosts, obviously varies considerably during seasonal changes. The writer (1957) has found evidence that in the Dragonette (*Callionymus lyra*) heavy infections of the gall bladder with myxosporidia, and concurrent light infections of the blood with haemogregarines, occur most abundantly during the winter in England, but in the same host the numerical relationships between these 2 protozoan parasites are reversed during the summer. These and other observations suggest that a heavy infection of one species of parasite is not ordinarily accompanied by heavy infections of another species, and that an active predatory habit with a taste for a wide variety of food predisposes to heavy parasitization. Such conclusions, however, can only be tentative pending much more study.

The ubiquitous and hardy Stickleback (*Gasterosteus*), with its delightfully interesting nest-building and other habits and its ability to wander from fresh to salt water and back again, has been the object of hundreds of studies on hydrobiology and on parasitism. This fish is apparently a "willing" host to dozens of protozoa and worms, and it occasionally becomes the victim of pathogenic parasitism. Limnologists often study sticklebacks in relation to the usual environmental features of a stream, but the relationships of the burden of parasites to the available food supply of the fish is often overlooked. The fish, in turn, is part of the food supply of numerous birds and other larger animals which thereby acquire larval parasites that grow to maturity in the new host, and influence markedly its metabolism and often its behavior.

The parasitic fauna of 4 fishes in the Volga Delta was studied by Dubinin (1949) who observed that changes in the numbers and kinds of parasites were closely bound to feeding habits and general way of life. *Cyprinus carpio, Abramis brama, Lucioperca lucioperca* and *Silurus glanis* were investigated, and the author found that fishes that go into hibernation in holes in rocks during the winter, and stop feeding, tend to lose their trematode and nematode parasites by January. The habits of developmental stages of these parasites are of fundamental importance in maintaining infections. In species of fish that do not stop feeding during the winter, infection with endoparasitic worms is retarded and the parasites remain for a longer time in their hosts. Although cold weather usually slows the development of both host and parasites, this effect is apparently reversed in the case of leeches and the crustacean *Argulus* ("carp louse"). In the latter instance the parasites are found crowded together and are actually more numerous than they are in warmer weather. *Argulus* injures the integument of its fish host, and it may cause the death of the fish during hibernation, or it may invite secondary infections.

In routine ecological investigations the ages of the fishes generally are not considered in relation to their parasites. Parasitologists, however, have often used fishes as a basis for the study of the effects of host age on parasitism. As a broad generalization we may say that the numbers of parasitic species in most fishes increase regularly with the age of the host. The average numbers of worms per freshwater fish usually show a regular increase with age and size of fish. Such worms as the tapeworm *Diphyllobothrium,* and the nemas *Camallanus* and *Rhaphidascaris,* and the flukes *Tetraonchus, Dactylogyrus* and *Azygia,* increase both in numbers and effects on their fish hosts with the fishes' age. Gorbunova (1936) has shown that the fish *Thymallus vulgaris* up to one year old has 7 species of parasites, but the yearlings of this host, in the period of transition to intense benthos feeding, enter conditions favorable to infection with many new nematode and trematode parasites. The nematode *Rhabdochona dentata,* however, decreases rapidly in numbers during the 2nd year, and at the age of 3 years the fish is free from this parasite. Two year fish appear to be the most exposed to infection by a number of parasites. At the age of 3 years the fish acquires some worms characteristic of adult fishes, but the hosts become less heavily infected with ectoparasitic trematodes and more heavily infected with the nema *Spiroptera.* Forty eight worms were found in one fish of 2 years as compared with 500 worms in a 3-year old fish.

Over a 3-year period a total of 4,532 freshwater fishes of northwestern Wisconsin were examined by Fischthal (1953). Worms, protozoa, copepods, glochidia, leeches and one virus were reported, but by far the largest number of species of any one group of parasites belonged to the trematodes. The greatest numbers of species of parasites found were larval or other immature stages of species whose adults are not normally encountered in these fishes. The observations suggested that fishes serve more commonly as intermediate hosts for worms than they do as final or definitive hosts.

The environmental factors which influence the growth and development of parasites on or in fishes are numerous and variable, but among those listed by Fischthal as particularly important are the following: (1) Greater biological productivity is favored in a lake or stream where the photosynthetic zone is closely superimposed over the decomposition zone, and if a lake basin edge is steep much of the essential decomposition materials is removed to deep water where it is inaccessable. As a consequence, the mollusks, turbellarians, annelids, insects and crustaceans which may be utilized as intermediate hosts for trematodes or cestodes find living conditions untenable. (2) Where there is an irregular shoreline with resulting bays, coves and shallow water there is a greater diversity of bottom and margin conditions. These conditions favor an abundance of plankton and larger plants and animals, including parasites in all stages of development. (3) When heavy snow blankets the ice on a lake or pond, a prolonged decrease in light occurs and this decrease results in a winter-kill which destroys many free-swimming larval stages of parasites as well as their fish hosts. (4) Among the chemical factors which affect the plankton containing larval parasites and their hosts are dissolved oxygen, carbonates, hydrogen ion concentration and numerous pollution influences from sewage and industrial wastes.

The Mud Sucker or Long Jawed Goby (*Gillichthys mirabilis*) has a parasite-mix consisting of at least 15 different species of protozoa, worms and anthropods. The host is common in estuaries along the coast of central and southern California and it is remarkably tolerant of changes in water salinity and temperature. Its parasites, for the most part, are equally tolerant of these changes, even those on the gills where the slightest chemical changes in the water are immediately felt. The fish serve as food for birds such as herons and undoubtedly many of its metacercariae find in these birds the compatible environments for final adult maturity. Obviously the snails and other invertebrates in the estuaries must also be tolerant of salinity and temperature changes if the larval parasites which utilize these invertebrates as intermediate hosts are to survive. In an estuarine area less than a half mile square, where several small, shallow streams flow into a main channel, there apparently are sufficient numbers of different and separated habitats to maintain a slightly different and characteristic parasite-mix for each habitat where *Gillichthys* is found.

PARASITE-HOST SPECIFICITY

Although some cases of strict host-specificity exist, most parasites are able to live and develop normally in 2 or more species of hosts. Host-specificity is fundamentally a function of physiology and of evolution, and the explanations of this phenomenon are, therefore, to be found in experimental studies in biochemistry of parasites and and of their hosts. Parasite-host specificity may be divided into 2 broad categories. The first is *ecological specificity,* wherein the parasite is capable of living in a foreign host but normally never reaches one because of an ecological barrier. Metacercariae from a fish can often be fed to chicks or young ducklings and grow to maturity in the gut of the foreign host. The second category is *physiological specificity* wherein a parasite is incapable of surviving in a foreign host because of physiological (=genetic) incompatibility. When physiological specificity involves a pattern of *behavior* it may be called *ethological specificity.*

Ecological aspects of host specificity can be studied effectively by introducing parasites experimentally into foreign hosts and then analyzing the reasons for failure or success in establishing a permanent relationship. Parasites can easily be fed to or injected into foreign fish, but one finds difficulty in establishing adequate criteria for determining "success" of the parasite in the new host. Even in normal hosts criteria such as volume of egg production, parasite size and number, are extremely variable. One must keep in mind the fact that success in any parasite-host relationship depends on ecological factors provided by *both* members of the associating pair.

The more primitive monogenetic trematodes are usually to be found on the more primitive groups of fishes, and specificity is ecological or physiological, and of phylogenetic significance, but those worms favoring freshwater fishes are somewhat less host specific than those on marine fishes (Hargis, 1957). In comparison with monogenetic trematodes the digenetic trematodes of fishes are less host specific, in spite of their more complicated life histories involving one to 3 transport (=intermediate) hosts. Nevertheless, among some fish parasites there exists a fastidiousness with regard to hosts. For example, 5 genera and 10 species (all host-specific) of the trematode family Accacoeliidae inhabit the intestine of the Sunfish *Mola mola.* Host-specificity among digenetic trematodes is greater among intermediate hosts, especially snails, than among fishes which serve as final hosts. Two distinct species of worms may live together without apparent antagonism in the gut of a fish, but each worm may require a different species of snail in which to undergo its larval development.

DISTRIBUTION

Distribution of parasites within a host is controlled by the same basic forces that govern distribution of the hosts. Temperature, moisture, mechanical barriers, chemistry of surrounding medium, food supply and other ecological factors continuously restrict or encourage the movements, growth or development of parasites. In the fish, *Gillichthys mirabilis,* mentioned above, 2 closely related nematodes live in the mesenteries, but only one of these worms is also occasionally to be found in the lumen of the intestine. A physiological difference between the 2 worms must be the explanation of this difference in distribution in the host because both worms appear to possess equal opportunity and equipment for penetrating the bile duct or the intestinal wall.

Migratory fishes and their parasites provide the ecologist with excellent opportunities to study the effects of changes in external environments on living organisms. Fishes such as tuna, salmon and eels that migrate for thousands of miles commonly acquire different parasites in different environments, although some of their parasites stay with the host no matter where they go. Such changes in parasite faunas are particularly marked when anadromous fishes are involved, but relatively few studies have been made of this problem. Most of the digenetic trematodes of eels are of a marine character, but adult female eels tend to lose their marine worms and to hold on only to freshwater species. Male eels, on the other hand, keep both marine and freshwater species (Dogiel 1936, Manter 1944). Migrating salmon acquire thousands of metacercariae whenever they enter freshwater but lose them during the marine wanderings. The small codfish *Eleginus navaga* of the Dvina Estuary of the White Sea is lightly infected with marine parasites, but heavily infected with freshwater species (*e.g.* the fluke *Diplostomulus spathaceum*). When the cod migrates toward the sea its marine parasites increase in numbers and in kinds. In the same estuary the herring which live in more salty areas are richer in marine species of parasites (Shulman and Shulman-Albova 1953).

The process of acclimatization to a new environment typically leads to impoverishment of the fish's original parasites, but a few relics of the past often remain. A host usually has a larger burden of parasites in the habitat where it has lived the longest. To give but one example, the fish *Lota lota* has numerous parasites characteristic of other freshwater fishes living in the same locality, but *Lota lota* is a member of the Gadidae, a family consisting almost exclusively of marine fishes, and it harbors some parasites whose anatomical features are reminders of its phylogenetic past.

SOME QUESTIONS TO BE ANSWERED

This brief mention of some of the more significant and interesting aspects of fishes and their parasites in relation to general hydrobiological studies may encourage the ecologist to consider such questions as those listed below whenever he encounters fishes during his field studies.

How does the presence of a population of one species of parasite influence the growth and development of another species in the same host organ or in another organ of the same host? What effect does seasonal change have upon the numbers and kinds of parasites for each fish? Are the parasites more tolerant or less tolerant than is the host to changes in the environment? Do the limiting factors of the hostal environment also directly limit the growth and development of the parasites? How do population changes in the host influence populations of its parasites? What are the size and age relationships between hosts and parasites? What changes in numbers, kinds and development of parasites are the result of migration of the host? What is the relationship between the food of the host and the kinds, number, and development of its parasites? How widely is the parasite distributed and what barriers prevent its further distribution?

Some of the questions require for their answers the services of trained parasitologists, but the simple asking of the questions by an ecologist could easily broaden the basis for judgments that lead to valid conclusions. As Audy (1960) has said, the biologist who is not a parasitologist is not accustomed to using parasites as "ecological labels" which provide an abundance of information about the habits and habitats of their hosts—information waiting to be tapped.

SUMMARY

A study of parasites with their hosts is a study in ecology because each member of the associating pair is part of

the environment of the other member. The parasite-mix is the total parasite fauna and flora of any plant or animal. The parasite-mix of fish gills has been described, and mention made of the kinds of parasites which may be encountered in other organs of fishes. In host organs burdened with a number of parasites a ferment of activity is continuously taking place involving competition for space and food, and the production of enzymes which effect profoundly both host and parasites. The kinds of food surrounding fishes are of prime importance in the problem of maintaining adult parasites, and the influences of seasonal changes in temperature and light serve to alter markedly the parasite-mix of fish hosts. The older the fish the more parasites it normally has, but migratory fishes often change the nature of their parasites as they move from one habitat to another. The process of acclimatization to a new environment usually leads to impoverishment of the fish's parasites. Although fish parasites may be gained or lost during environmental changes, some of them are host-specific (*e.g.* monogenetic trematodes), but most of them are able to live and to develop normally in 2 or more species of hosts. The use of parasites as ecological labels provide an abundance of information about the habits and habitats of their hosts.

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GRASSLANDS[1]

There is an increasing awareness of the value of grasslands in the production of food for an expanding world population. What is not always realized, however, is the complexity of the grassland ecosystem (climate, soil, topography, vegetation, the grazing animal, and other biotic factors) and the fact that for proper understanding and development of its full potentialities, research in a wide field of scientific disciplines is essential. The value of grasslands is in large measure determined by the animal products obtained, but other values such as soil conservation and the maintenance of soil fertility and structure must not be neglected.

The AAAS is to be commended for organizing a symposium in which experts in many disciplines were brought together to discuss grassland research. Publication of the proceedings of the symposium makes the contributions available to a much wider group. Howard B. Sprague states in the preface, "Although some areas of knowledge affecting grasslands are not represented in these selected papers, this volume should prove helpful to the large group of scientists who are desirous of keeping abreast of progress in the broad front of grasslands research, beyond the field of their own specialization." It was apparently intended that the papers be "reviews of current development in specific areas of subject matter." The value of some contributions would have been enhanced by a more critical appraisal of the work quoted, and by drawing on a wider field of literature. A number of contributors have stressed the need for greater attention to both cooperative and basic research.

The book comprises 37 papers grouped into 8 sections. The wide range of subject matter in itself indicates the complexity of grassland research. The preface in part seeks to emphasize the interrelationships of the scientific disciplines involved, and the necessity for cooperative research, but these important aspects could have been more forcibly brought to the attention of readers. If time was allowed at the symposium for discussion of individual papers, it is perhaps unfortunate that the salient features of the discussion were not reported. It is unlikely that some of the statements made were left unchallenged.

As is to be expected, the quality of the papers presented is varied, but it would be impossible for any one person to give a critical review of each paper. An attempt will be made to indicate the nature of the contributions to each section, and to summarize, in the opinion of the reviewer, some of the more important concepts and conclusions reached.

I. Sciences in Support of Grassland Research.—Papers on plant exploration, integration of genetics, pathology and entomology, interrelations of physiology, ecology and soil science, plant nutrition, and microclimate are presented. Rapid advances in forage crop improvement could follow an ambitious and intelligent program of plant introduction. Close cooperation between the plant breeder, pathologist, and entomologist is needed for developing disease- and insect-resistant varieties. A more basic approach to both plant and animal nutrition is required. The close relationships between microclimate and grassland management and production, and the need for further research, are clearly indicated.

II. Forage Production in Temperate Humid Regions.—Grasslands of the corn belt and of the northeast, development of improved varieties of forage crops, disease and insect control are discussed. There is emphasis on the development of improved varieties and strains of forage species for increased production and for the control of disease and insect pests. Greater emphasis might have been placed on the requirements of the animal and the problem of extending the growing season of forage species.

III. Engineering Aspects of Grassland Agriculture.—Contributors report on equipment for establishment and maintenance of grassland, for harvesting, transporting, preserving, storing, and feeding of silage and hay, and for irrigation of grassland. One author was concerned about the lack of a satisfactory definition of hay quality, which hampers the development of the most suitable equipment, and with the avoidance of waste during the making, transporting, and feeding of hay.

IV. Forage Utilization and Related Animal Nutrition Problems.—Forage utilization for dairy cattle, nutritive value of forages, mineral problems, and estrogenic substances are discussed. Good quality hay or silage is more economical than feeding concentrates to dairy cows. It is proposed that estimation of the nutritive value of a forage be based on its polysaccharide content. Mineral composition of pasture is important in utilization, but the problems are complex, involving deficiencies, excesses, and balance. Because some pasture species contain estrogenic or other harmful substances, reliance should not be placed on single species, and agronomists, plant breeders and others must consider the effect of a species on animal health.

V. Evaluation of the Nutritive Significance of Forages.—Determination of nutritive value of forages, evaluation of energy in forage, and effect of stage of maturity and other factors on feed value of forages are discussed. Forage evaluation requires basic studies in ruminant physiology. Suggestions are made for improved methods of forage evaluation, based on digestible energy. Many problems remain to be solved, and some lines of future research are indicated. The effect of stage of maturity of forage on digestibility and utilization is also considered. There was no indication that this work should ultimately be extended to field conditions, where the problem is immensely complicated by the variety of food presented to the animal, and by the animal's ability to select its diet.

VI. Grassland Climatology.—In this section both macro- and micro-climatology are discussed in relation to grassland. Natural grasslands are related to climatic factors, particularly moisture supply and temperature. (The reviewer would suggest, however, that the situation has been oversimplified by too ready a dismissal of fire, biotic, and other factors). Large areas of grassland have been developed following the destruction of forests or other natural communities, and are maintained where soil, climatic and economic factors are favourable. Microclimatology is discussed in relation to vegetation, and the possibility of using different topographic situations for different types of grassland becomes clear. One author points out that the climatologist does not know enough about related disciplines, nor about management problems to which he could contribute.

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[1] Sprague, Howard B. (editor) 1959. Grasslands. A symposium presented at the New York meeting of the American Association for the Advancement of Science, December 27-30, 1956. xv + 406 pp., 37 illus., ref., index. Publication no. 53 of the AAAS, Washington, D. C. $9.00.

VII. Ecology of Grasslands.—This section comprises four stimulating papers dealing with the effects of changes in weather conditions on grasslands, plant succession and range improvement, ecological principles in range evaluation, and the nature of the grassland community. Studies of the effects of alternating drought and humid periods emphasize the dynamic nature of the equilibrium between community and environment. A discussion of plant succession in relation to range improvement highlights facts and ideas which should encourage a more realistic approach to range research. An outline of the procedure developed by the Soil Conservation Service for range evaluation, based on quantitative synecology, is given, and the method reviewed in the light of certain basic ecological principles. In the concluding paper it is shown that wide genetic variability within a species enables it to survive in a wide range of environmental conditions. Many detailed ecological investigations of grasslands aimed at obtaining basic data are required.

VIII. Range Management.—In this section the papers cover the breeding and testing of range forage plants, soil-vegetation survey, effects of climate and grazing on mixed prairie, brush control, and improving range resources through management. Breeding of improved varieties of forage species for western ranges has given promising results, and extensive range improvement can be anticipated following further work. Adequate testing of varieties is essential, including the testing of nutritional quality and drought resistance as well as total production. Soil-vegetation surveys provide permanent basic data for land-use planning. Recovery of a moderately grazed prairie following drought can be expected, but combined drought and heavy grazing are likely to be disastrous. Invasion of many western ranges by shrubs and trees has followed heavy grazing of the range and the lowering of fire frequency and effectiveness. Basic ecological and range management studies in these communities are required. Range resources can be improved by the application of suitable management practices, with increased forage and livestock production and higher net economic returns.

The symposium was organized in the U.S.A., and contributors have concentrated on the American scene, but this does not detract from the value of the book to workers in other countries. Perhaps other groups will be stimulated to organize similar meetings. If so, one may hope for publication of the proceedings of such meetings to facilitate dissemination of the results of research and profitable avenues of future work amongst a wide range of specialists in many scientific disciplines throughout the world. Howard B. Sprague is to be commended for bringing to completion a difficult task with the publication of a book which not only should be consulted by all interested in grassland research, but also sets a high standard for any future publications of this type.

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AUSTRALIAN ECOLOGY AND BIOGEOGRAPHY[1]

This volume is a collection of 37 contributions covering a wide range of topics in pure and applied zoology and botany. It would appear from the introduction by the Series Editor that it was originally intended to be zoological only. And indeed the nucleus of the collection seems to be an introductory general article by the zoological editor (A. Keast), followed by a group of papers dealing well and reasonably consistently with the zoogeography of different animal groups in Australia (marsupials by E. le G. Troughton; birds and reptiles by A. Keast; fresh-water fishes by G. P. Whitley; Homoptera and some other insect groups by J. W. Evans; Diptera by S. J. Paramonov; Mollusca by D. F. McMichael & T. Iredale; and Crustacea by E. F. Reck). Littoral and marine organisms are excluded throughout, and discussion is mainly confined to the continent itself, with frequent references to Tasmania, but few to New Guinea despite its fairly close biogeographical relation to Australia. Outside this zoogeographical nucleus the editorial grip seems to have weakened, and the rest of the book consists of a miscellany of articles only vaguely held together by the guiding theme. The order of the articles, too, could have been better thought out; it would be logical for discussions of the physical environment to precede descriptions of vegetation, which would themselves form a useful preliminary to discussions of animal ecology. As it is, the order of the articles makes it difficult to follow them in sequence, and makes a certain amount of repetition inevitable. In these respects the book is bound to be compared unfavourably with THE AUSTRALIAN ENVIRONMENT, of which a new edition has just appeared, and which in part covers the same ground.

Within the range of subject matter included, there are notable gaps. Some of the invertebrate groups (many insect orders, Arachnida, Myriapoda, the worms and the Protozoa) are not mentioned, nor are any of the lower groups of plants despite the considerable interest attaching to the Pteridophyta (for instance) in Australia. Even among the flowering plants, phytogeographical discussion is inadequate. Such considerations are included in C. A. Gardner's article on the vegetation of Western Australia, and briefly in A. B. Costin's on mountain vegetation; but there is nowhere, for instance, a list of Australian endemic families (A. Keast in his introductory article mentions their number as three, in contrast with the eleven recognized by Good). The distribution of the two most important genera (*Eucalyptus*

[1] Keast, A., R. L. Crocker, & C. S. Christian (editors). 1959. Biogeography and ecology in Australia. (symposium) Uitgeverij Dr. W. Junk (Monographiae Biologicae Vol. 8), Den Haag. iv + 640 pp., 56 figs., 18 pl. Hfl. 65., $17.10.

and *Acacia*) is, however, fully discussed by L. D. Pryor and the late J. G. Wood.

Turning to the ecological papers, one finds as expected that the influence of aridity is well to the fore, though Australia (contrary to general belief) contains few if any true deserts, and has barely 40% of its area (not "by far the major portion," as stated by Pryor on p. 463) within the 10-inch isohyet. On the other hand, the great influence of fire in determining the nature of plant and animal communities is hardly given the weight it deserves.

Plant ecology is not covered as well as might be hoped. Apart from the articles by C. A. Gardner and A. B. Costin already mentioned, some of the drier formations are discussed by N. C. W. Beadle and by R. M. Moore; but these articles are to be a considerable extent concerned with applied ecology—grazing utilization, and soil erosion. Pryor has some interesting thoughts on co-dominance and vicariousness in his article on *Eucalyptus* distribution. Coverage of plant ecology might have been more satisfactory had a consistent policy been adopted as to whether vegetation should be described region by region or formation by formation. Rain forests (tropical and temperate) are practically ignored, and coastal vegetation is hardly mentioned either. It is noteworthy that the articles on plant ecology, though often referring to degeneration under human influence or grazing pressure, seldom mention succession.

The ecology of certain animal groups is well described—for instance, marsupials (A. R. Main *et al.*), ducks (H. J. Frith), frogs (A. R. Main *et al.*), termites (J. H. Calaby & F. J. Gay), grasshoppers (K. H. L. Key) and sheep blowflies (K. R. Norris). There are also articles on bird-banding (R. Carrick), ornithosis of wild birds (J. A. R. Miles) and the physiology of marsupial reproduction (G. B. Sharman); the last—the longest article in the book—seems rather out of place.

The remaining articles may be divided into those discussing the physical environment, and human aspects. The former include L. Emberger's consideration of Australian analogues of the various climates in the Mediterranean region, R. L. Crocker's article on climatic fluctuations and past vegetation, and a discussion of soils by G. A. Stewart; geology is hardly represented. Human ecology in the period before European settlement is discussed by N. B. Tindale, and the general story is brought up to date by Griffith Taylor. Other special aspects of the interrelation of man with his environment are soil erosion (R. G. Downes) and the survey of undeveloped areas with a view to their possible utilization (C. S. Christian). Four introduced organisms which have had a marked impact on Australian ecology are the subject of special articles—the Merino sheep (I. W. McDonald); the rabbit (F. N. Ratcliffe), with special reference to myxomatosis; subterranean clover (F. H. W. Morley & O. H. Frankel), and the evolution of local strains; and prickly pear and its control (A. P. Dodd)—still very interesting, though now rather *vieux jeu*. These four articles could well have been supplemented by one on introduced weeds. The book concludes very appropriately with an article on nature conservation (R. Carrick & A. B. Costin), and it is to be hoped that this, at least, will be widely read by politicians and administrators in Australia.

Of the 34 articles by Australian contributors, 15 are written by officers of the C.S.I.R.O. (the Federal government's research arm), and seven by the staff of the Australian Museum in Sydney, leaving only seven by University personnel and five by others. Geographically, the unbalance among contributors is even more marked, for the great majority of the articles come from New South Wales (including the enclave of the Australian Capital Territory); there are only three from Western Australia, two from South Australia, one each from Victoria and Queensland, and none at all from Tasmania and the Northern Territory. This is paralleled in the emphasis of the subject matter. Tasmania and Queensland are neglected, and even Victorian experience is not drawn on as it might be—for instance, in Costin's article on mountain vegetation, and Pryor's on *Eucalyptus* species.

The documentation policy has been inconsistent. Some articles are without bibliographies; others have bibliographies which may include work not cited in the text, or fail to include work which has been cited. Some include titles, others do not.

The book is in general well produced, though a fair number of printing errors occur. A few photographic plates have been included, but considerably more use could have been made of this form of illustration, particularly in describing vegetation types. Some of the maps (notably some illustrating Griffith Taylor's article) are deplorably small; in a volume of this type (and at this price) a few folding maps on a larger scale would surely have been appropriate. There is an index, but it adds little to the table of contents; it includes no personal names and few generic names, and the entries present are often quite incomplete.

To conclude, one may say that this volume is poorly integrated, but contains many interesting and useful articles, covering fields not commonly brought together. Libraries with any interest in the subject will certainly wish to have it on their shelves.

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Forest Tree Physiology[1]

"Few plant physiologists use trees for experimental material, and few professional foresters study plant physiology." So begins the preface of an important book which records the proceedings of the first International Symposium on Forest Tree Physiology which was held at the Harvard Forest in April 1957. The symposium, which was sponsored by the Cabot Foundation, was a small one comprising 33 "active workers" mainly from North America, but with six from Europe and one from New Zealand. It aimed to give the "broadest possible coverage of the main areas of the field" of tree physiology.

The 35 papers which were presented at the symposium are all published in entirety and are followed by the discussions which ensued, in an abridged form. The book is divided into nine parts dealing with: water relations and sap movement; photosynthesis; general biochemistry; mineral nutrition; phloem transport; root growth; other growth phenomena; photoperiodism and thermoperiodism; reproduction. In a short review it is not possible to discuss each paper: comments will hence be restricted to some of the points which may be of interest to forest ecologists. The standard of the papers varies enormously from the uncritical presentation of the results of a series of experiments to the scholarly account of a piece of research.

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[1] Thimann, Kenneth V. (editor) with assistance of William B. Critchfield and Martin H. Zimmermann. 1958. The physiology of forest trees. A symposium held at the Harvard Forest, April, 1957, under the auspices of the Maria Moors Cabot Foundation. Ronald Press Co., New York. xvi + 678 pp., 226 figs., 66 tables. $12.00.

From experiments on pine seedlings, Stone concludes that water can be absorbed from a saturated atmosphere and that this process may be of considerable survival value. Krammer points out that whilst individual tree leaves might reach their maximum photosynthetic rate in one third or less of full sunlight, as a result of mutual shading of the leaves the tree as a whole often requires full sunlight to reach its maximum photosynthetic rate. Richardson shows that root growth in the winter is dependent on the physiological state of the shoot buds. By an ingenious technique, Leyton and Rousseau show that of six species they studied, only willow (*Salix atrocinerea*) has roots which can grow in anaerobic conditions. The papers on photoperiodism demonstrate that, generally speaking, long days promote vegetative growth and short days promote dormancy. The adaptation of trees to growing seasons of particular lengths by the process of natural selection is discussed by Pauley who concludes that there is strong evidence for this occurring in *Populus trichocarpa*.

The symposium was on the physiology of *forest* trees: presumably as opposed to fruit trees about whose physiology much more is known as is pointed out by several speakers and by the whole of Sax's paper. Trees, because of their size, are not particularly suitable experimental material. Trees in their natural habitats are even less suitable. This accounts for the use of seedlings for many of the experiments discussed at this symposium even though it is frequently pointed out that their responses may be quite different from the responses of mature trees.

It is felt that the symposium did, on the whole, present a good picture of current work on forest tree physiology. The idea of having only "active workers" at the symposium was a good one; for the discussions appear to have been of a high standard and, as was the one following Pauley's paper, extremely lively and controversial! Whilst most of the authors presented the results of their work against a general background of other work on their subject, the volume does tend to present accounts of various experiments rather than a concise account of the state of forest tree physiological research in 1957. Hardwoods and soft woods receive roughly equal treatment but, apart from Scholander's work on lianes, tropical species are excluded. This is unfortunate for although little is yet known about the physiology of trees in tropical forests the literature on some economic species, such as teak (*Tectona grandis*), is voluminous. Also a considerable body of data are being collected relating growth rates of rain forest species to environmental conditions—an aspect of temperate tree physiology neglected by the symposium.

The book is extremely well produced and it will serve as a useful reference book for plant physiologists, ecologists and foresters.

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MODERNIZING THE TAXONOMY OF CALIFORNIA PLANTS[1]

This new manual is a splendid help to ecologists interested in the flora and vegetation of California. At once it brings up to date the taxonomy and nomenclature of California plants, provides a reasonably portable handbook of such information, and includes much auxiliary data which have become a part of modern floras, such as morphology and variation, measurements of plant parts, distinguishing characteristics, keys, chromosome numbers, phenology, distribution, and habitats. Habitats are described by means of physical factors and by occurrence in one or more of 29 plant communities.

The last feature is unique in North American floras and is of particular interest to ecologists both for its own sake and because many phytosociologists have contended that the most objective indices to habitat are not factors of the environment or physiognomy of vegetation but floristically defined plant communities. Recognition of habitats by botanists should be easiest by means of associated plants.

The addition of plant sociological notes to descriptions of taxa is now a common European practice. Floras of Schleswig-Holstein by Christiansen, Germany by Rothmaler, southwest Germany by Oberdorfer, of the Alps by Fenaroli, the new Dutch and Lawalree's Belgian floras, and Braun-Blanquet and Rübel's flora of Graubunden are examples of general treatments (cf. EXCERPTA BOTANICA, SECTIO B 1(2):89-133, 1959). To these floras can be added Munz and Keck's. It is something of an anomaly that California, where the study of vegetation and of plant ecology have lagged so seriously, is the first area in North America to have a flora containing data on the vegetation or plant community relationships of its plants.

Unfortunately this classification has been done from the top, not inductively. It contains a very strong geographical element, which means that the communities are heterogeneous from both ecological and floristic standpoints. No inductive system would throw pond, cliff, scree, and forest vegetation together just because of spatial contiguity. Munz and Keck do. Plants of such specialized habitats as ponds, cliffs, screes, peat, serpentine, and streambanks suffer particularly in habitat description by being lumped in with a zonal kind of vegetation such as a particular kind of forest. Secondary vegetation is also neglected in this community classification. The plant communities used by Munz and Keck are quite broadly conceived, being equivalent probably to European orders or classes.

Although Munz and Keck's flora describes the habitat distribution of each taxon excellently by means of vegetation associations, it is less adequate for purely chorological distributions. Chorology is better described by definition and use of floristic regions than by using political boundaries. Such regions may coincide with vegetation regions but their definition is floristic—thus recognizing the primacy of floristic differences in work on vegetation. These means of describing the ranges of plants are used in floras of the USSR and the Greenland flora. Still more precise, and least misleading, would be dot maps of all occurrences which are known, as in Hulten's work, or an equivalent system of mechanical subdivision of a country as in Christiansen's flora of Schleswig-Holstein or the Dutch, Danish, and Belgian floras, or the distribution maps scheme of the Botanical Society of the British Isles. All such more precise data would act as a great stimulus to increases in floristic knowledge. With Munz and Keck's new flora as a basis, such more precise chorological information for California plants is a practical goal.

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[1] Munz, Philip A. in collaboration with David D. Keck. 1959. A California flora. University of California Press, Berkeley & Los Angeles. 1568 pp., 143 figs. $11.50.

Ecological peculiarities in treatment of taxa should be noted. Relationships to particular soil properties such as abundant nitrogen, acidity, serpentine, alkali, saline conditions, etc. are frequently not mentioned, and the ecologist would appreciate the mentioning of specific kinds of soils such as chernozems, podsols, etc. if it is really impossible to mention soil series. Additions to the species descriptions might include life-forms, pollination mechanisms and agents, and means of seed dispersal. As to particular taxa, the genus *Torreyochloa* is submerged in *Puccinellia* resulting in what is certainly a most odd genus from the standpoint of ecological and distributional homogeneity. In California *Puccinellia*, then, is said to consist of 6 plants of lowland, alkaline habitats and 3 of montane or even alpine habitats. There is a very great ecological difference between *Puccinellia* and *Torreyochloa*, and it holds also outside of California. Again *Arctostaphylos sensitiva* is ecologically well-differentiated from *A. nummularia*. To include the former as a variety of the latter is to disguise their ecological distinctness. To miss the association of such species as *Aristida oligantha* and *Oenothera ovata* with spring seepage areas, although such sites may be very dry later, is to obscure their ecological relationships. The treatment of lodgepole pine seems unsatisfactory. Critchfield (1957) recognized 4 subspecies, Rocky Mountain *latifolia*, Sierran *murrayana*, coastal *contorta*, and *bolanderi* on the Mendocino Co., California podsols.

Mechanically, the book is good. It is not really gross considering the great mass of information contained. Taxonomically, the book has few name changes, and many are based on new knowledge about the plants. Some readers may miss common names altho such vernacular names as "Douglas fir"—which incidentally is astonishingly more stable than any Latin name applied to this unfortunate tree—are given. The phylogenetic order of families is new and offers a fresh field for agreement among taxonomists now they have disposed of the problem of stabilization of species names by refusing to consider the problem further.

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EVOLUTION IN A FAMILY OF ANGIOSPERMS[1]

The family Polemoniaceae is of only moderate size compared with many groups of flowering plants, but it poses a number of remarkably difficult problems in classification, at every taxonomic level from the tribal down to the subspecific. Its genera are not sharply delimited morphologically, so that different taxonomists working with the family have varied between extremes of "lumping" species in a few large genera or "splitting" them among many smaller ones. Differences between species, as well, are often blurred, perhaps through natural hybridization; but on the other hand, closely similar entities exist which can be recognized as distinct species only by careful field studies of sympatric populations. These and other aspects of the variation seen in the phlox family suggest that evolutionary change and speciation are actively occurring in many of its generic lines, so that the family presents itself as a favorable object of study for systematists interested in the process of evolution, itself. Verne Grant has been a leader for over ten years in the experimental study of evolution in the Polemoniaceae. In this first volume of a two volume series he begins an inclusive survey of all aspects of its natural history in order to develop the family as a model of evolution in a group of higher plants.

In concentrating on a single systematic group and attempting to explain its evolutionary pattern as thoroughly as possible, Dr. Grant finds precedents in works like those of Babcock with *Crepis*, Goodspeed with *Nicotiana*, and Blakeslee with *Datura*. Because it encompasses an entire family of plants, however, Grant's study may have wider application in evolution theory than these earlier generic monographs. The success of Grant's project will best be judged when the second volume is completed, and it is helpful to note here the sequence of presentation he has chosen for the whole opus. In this first volume there is a nearly complete taxonomic treatment of the family, sparing only keys and species descriptions (references are given to the most recent monographs of each genus). Additional chapters deal with morphology, chromosome numbers and karyotype evolution, phylogeny, and phytogeography including migrational history. The volume as a whole thus contains most of the essentially descriptive studies that form a groundwork for the detailed experimental findings to be reported in the second volume. In the latter, Grant intends to take up the subject of the reproductive biology of the phlox family, to include life cycles, pollination, breeding systems, genetic structure of populations and of races and species, fertility relationships, and adaptive radiation in the reproductive system. The completed work should be an inclusive view of the mode of evolution in this one family of angiosperms.

For the readers of ECOLOGY it should be pointed out that over half of the volume at hand, some 150 pages, is devoted to reference material of special interest to taxonomists and specialists in floristic research. The chapters on problems of classification, synopses of genera and sections, lists of synonyms, indices, and documented chromosome numbers need not be reviewed in detail. Grant presents persuasive arguments for his solution to the controversial problem of delimiting tribes, genera, and sections. His list of recognized species is only tentative, however; "the task of straightening out the species and subspecies of the Polemoniaceae is still in its initial stages," (pg. 45). Certain innovations in the presentation of the taxonomic portion—separating the descriptions from all the synonymy; using tabular comparisons rather than keys—seem to be convenient, and the illustrations of selected species are excellent. However, an artificial key to the genera would have been a valuable addition, I believe; using Grant's natural synopses and descriptions alone, one might have difficulty placing an unidentified plant with certainty, even to the correct tribe.

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[1] Grant, Verne. 1959. Natural history of the Phlox family, Volume 1. Systematic botany. Martinus Nijhoff (International Scholars Forum, Sciences, Vol. 1), The Hague. xv + 280 pp., 79 figs., 14 tables. Hfl. 19.—, $5.00.

It is in the sections dealing with phylogeny and phytogeography that Grant develops concepts having the most interest to ecologists. His method of attacking the basic evolutionary problems of phylogenetic trends, parallelism, centers of origin, and migrational history is through carefully reasoned deductions based on the comparative morphology and distribution of living forms (there is no significant fossil record). In these deductions ecology is found to play a major role. Because the locale for evolutionary diversification of the Polemoniaceae, from Early Tertiary onward, has been the Western Hemisphere, the climatic and physiographic history of this region is intimately connected with the phyletic history of its flora. Evolutionary trends in morphology can be read in only one general direction—woody plants with generalized vegetative and reproductive organs *to* herbs with specialized leaves, flowers, and fruits—because of the known historical trends in habitat diversification and specialization in the New World. In the oldest environment, the montane tropical rain forests, are species of Polemoniaceae that retain many primitive vegetative and floral features; more derived species in temperate forests and arctic habitats probably evolved after a quantum shift to tolerance for cooler climates; and the highest specialization of types occurs in the more recently formed arid habitats of western woodlands, scrub, and deserts. The two largest phyletic lines, the tribes Polemonieae and Gilieae, are outgrowths of the family's evolutionary response, as it were, to the ecological combinations of cool-moist-temperate and warm-dry-subtropical, respectively.

A more detailed account of the history of the Gilia Tribe is possible through its close connection with the Madro-Tertiary Geoflora, the evolution and migrations of which have been described by Axelrod. From shrubby plants of the summer-moist Sierra Madrean woodlands there evolved in California, during the expansion there of the Madro-Tertiary flora, morphologically specialized herbs adapted to conditions of moist, mild winters and dry, hot summers. The rapid development of desert habitats in the Late Pliocene favored the evolution, from these Californian Gilieae (already adapted to sandy soils), of highly reduced, frequently self-pollinating, ephemeral annuals. Accompanying the rich speciation in these arid communities are such taxonomically complicating factors as ecotypic differentiation, interspecific hybridization, and polyploidy. Many of the topics to be reported in Grant's second volume deal with the adaptive changes in breeding systems, karyotypes, and genetic systems found in these complex, rapidly evolving species.

That phylogenetic speculations ought not to be made without reference to ecological data is, of course, obvious. Grant's reconstruction of the history of the Polemoniaceae is an appealing synthesis of knowledge, in which the interaction of internal, genetic factors and external, ecological ones is always evident. Certain aspects of the natural history of this family seem still to be relatively neglected, however. Further progress may come, as Grant himself suggests, from intensive investigations of comparative morphology. Almost every part of the plant, from wood to trichomes, needs more detailed study. If this work lacks some of the glamour of experimental systematics, it is hardly less important to our knowledge of evolution. Natural selection still acts, first of all, on the phenotype.

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BEHAVIOR AND EVOLUTION[1]

The results of two joint conferences between the American Psychological Association and the Society for the Study of Evolution have been summarized in this volume. The two conferences were sponsored by the National Science Foundation and the Rockefeller Foundation. The first conference was held at Harriman, New York in April 1955; the second, involving mainly the same participants, was in April 1956 at Princeton, New Jersey. In order to leave time for discussion at the second conference, authors made advance drafts of their papers available to other participants, and presented only the gist of the papers at the meeting. Each paper is followed by an extensive bibliography, and a complete and detailed index concludes the volume.

Most of the papers presented and discussed at the meetings are printed. They are arranged under five topics: the study of evolution and its record; the physical basis of behavior; categories of behavior; the place of behavior in the study of evolution; and evolution and human behavior.

In Part I the synthetic theory of evolution is evaluated and its implications examined through the insights of three leading paleontologists. George Gaylord Simpson traces the evolution of evolutionary theories, and attempts to organize a few generalizations and evolutionary principles. Edwin Colbert's thesis that behavior patterns of living animals can be interpreted only in terms of the morphological evolution of the animal, is illustrated by a discussion of dinosaur behavior. Through his discussion of phylogenetic increase in complexity of locomotion and feeding and correlated nervous control, A. S. Romer demonstrates the truism that development of behavior depends upon development of the mechanisms of behavior.

In Part II these behavior mechanisms are reviewed by

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[1] Roe, Anne and G. G. Simpson (editors) 1958. Behavior and evolution. (symposium). Yale University Press, New Haven, viii + 557 pp., figs. $10.00.

Frank Beach, Ernst Caspari, R. W. Sperry, Karl Pribram, and T. H. Bullock, the general thesis being that the physical basis of behavior is the functional anatomy of the behaving organism. Beach points out that while there is basic chemical similarity in male sex hormones throughout the vertebrate classes, the type of behavior elicited varies widely. Bullock argues that the relationship between mind and brain evolves as an aspect of physiological and morphological evolution. He excuses the neuron, as currently understood, from responsibility for behavior.

The offerings of descriptive material in Part III come from both psychologists and systematists, in harmony at least in their aim to find explanations and relationships within behavioral repertories. Henry Nissen offers criteria for the classification of behavior and points out that behavior and morphology present alternate means of adaptation. Phylogenetic comparisons might be made in terms of behavioral function as well as on basis of mechanisms used, he feels. Other contributors to this section are Marston Bates (food-getting behavior), C. R. Carpenter (territoriality), Hinde and Tinbergen (species-specific behavior), Harlow (evolution of learning), William Thompson (social behavior), and Alfred Emerson (evolution of behavior in social insects).

In Part IV the symposium finally gets around to asking whether or not a symposium on this subject is justified, and the answer provides a unifying discussion of the relationships between psychology and zoology. In his consideration of systematics, Ernst Mayr deals with the value as phylogenetic clues of conservative behavior elements, and points out that responses to environmental stimuli are more subject to change than are innate elements of behavior. His emphasis on genetic variability has particularly strong implications regarding evolution. Herman Spieth points out that among a number of isolating mechanisms between closely related sympatric species, behavioral characters may be the most effective deterrents to interbreeding. Colin Pittendrigh concludes the section with a discussion of the philosophy and practice of adaptation.

In Part V, Margaret Mead, Julian Huxley, L. Z. Freedman and Anne Roe, and S. L. Washburn and Virginia Avis tackle the difficult area of human behavior, where factors of cultural inheritance complicate not only the task of studying behavior but also the task of being integrated humans. The evolution, adaptation and natural selection of cultural characters reemerge as a legitimate area of study.

G. G. Simpson's epilogue, organized around the headings of biological significance of behavior, ontogeny of behavior, and evolutionary principles and behavior, binds together the often divergent ideas of the symposium. He concludes by regretting the omission of that behavior characteristic "best exemplified in and by this book—exploratory curiosity."

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BEHAVIOR OF THE INVERTEBRATES[1]

Some of the most fascinating studies of animal behavior have been done with insects, but the behavior of most non-arthropod invertebrates has scarcely been touched. This contrast is sharply brought out in the recent book by Professor J. D. Carthy which brings together a large amount of information on sensory physiology and behavior of invertebrates, particularly the insects. As the author points out in his introductory remarks, "The mass of work still waiting to be done on invertebrates other than insects stands accentuated once again."

The book is strongly slanted toward sensory physiology and Carthy stresses throughout the importance of external factors in determining the behavior of invertebrates. After a brief introduction the author reviews the sense organs of various invertebrates ranging from the light-sensitive organelles of the Protozoa to the compound eyes and complex chemoreceptors of insects. Many of these sense organs are well illustrated by line drawings.

Most of the book is devoted to a series of chapters dealing with the perception of various stimuli and the corresponding responses of different invertebrates. A chapter on the light senses includes discussions of the influence of light on the aggregation of animals, the light compass reaction, and a general discussion of the role of simple reactions to light in the life of various invertebrates. The following chapter deals with the perception of color and polarized light. A subsequent chapter contains a discussion of the perception of form and movement.

One of the best sections of the book is in the discussion of polarized light, where Carthy gives an excellent review of the navigation of sandhoppers as well as a brief account of the well known studies of bees. In the three chapters dealing with the light senses, as elsewhere, the author points out serious pitfalls in behavioral studies and demonstrates a shrewd knowledge of the limitations of experimental situations.

The latter half of the book covers reactions to heat, gravity, vibrations, touch, chemicals, and humidity. Each chapter begins with a discussion of the nature of the stimulus and some of its physical properties. Most of these introductory discussions are well done but the author falters in attempting to distinguish between heat, temperature, and heat capacity.

Most of the examples cited in the chapter on heat indicate that the reactions of invertebrates simply serve to bring them into or keep them in the optimal temperature range. Several parasites, however, respond to the warmth of the host's body and this seems to be an important mechanism in host detection.

Many examples are drawn from different phyla to illustrate reactions to gravity although in some forms, notably among the Echinoderms, the sensory basis for reactions to gravity is uncertain. Because of the absence of clearly-demonstrated tympanic organs outside the insects, the discussion of sound is limited to insects. Several examples are cited to illustrate the role of sound in courtship, location of prey, and the detection of predators.

In his discussion of the chemical senses, the author

[1] Carthy, J. D. 1958. An introduction to the behaviour of the invertebrates. Macmillan, New York & London. xi + 380 pp., 148 figs., 15 tables, 4 pls. $8.00.

attempts the difficult distinction between taste and smell and arrives at the operational definition that, "In general smell leads to locomotion as it is used to distinguish substances at a distance . . . . while taste, the contact sense, is particularly concerned with eating and therefore stimulation of these receptors often leads to feeding movements." His examples of olfaction are wholly drawn from the extensive work on chemoreception in insects while the discussion of taste includes examples from several invertebrate phyla. The discussion of humidity sensitivity centers upon the problematical mode of action of humidity receptors in the insects.

In the final chapter, Professor Carthy discusses "Whole patterns of behavior." Here the author points up the wide range of complexity of behavior in the invertebrates and stresses the adaptive value of variability in reaction to stimuli. He also cites a few examples to illustrate the interplay of reactions to various stimuli in nature.

Professor Carthy has brought together in this book an important body of information (documented by 591 literature citations) on sensory perception and its role in the behavior of the invertebrates. For this reason the book is a valuable contribution and a useful beginning toward a comprehensive picture of invertebrate behavior. Because of the neglect of most aspects of behavior other than the physiological and the absence of adequate information on the behavior of many invertebrates, however, the author arrives at something less than an adequate "introduction to the behavior of the invertebrates." Detracting from the potential usefulness of the book also are a number of minor errors, mainly incorrect citations to the extensive bibliography.

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FAUNA HYGROPETRICA UPDATED[1]

The recent publication of a significant paper by F. Vaillant on the fauna of steep, wet-rock surfaces (Thienemann's "fauna hygropetrica") serves to focus much-needed attention on one of those rare biotopes which, like springs, bogs, and tree-holes, is environmentally and spatially so distinct from its surroundings that it fosters a biota which, in its relative simplicity and specificity, is something quite apart from all others. Discrete habitat units of this sort have traditionally drawn ecological interest all out of proportion to their significance in the economy of the biosphere, but have consistently justified such concentrated attention by serving as type-cases for important ecological principles.

It is strange, then, that so little work has been done on wetrock biotas. Thienemann's original paper[2], describing the habitat and listing its Central European inhabitants, was followed, over the years, by occasional contributions in his works on springs, adding new species to the list and noting that this water in nearly always supersaturated with oxygen. In addition he reëmphasized the special nature of this ecologic unit. Feuerborn's paper[3] on the larvae of German Psychodidae, a dipterous family whose members are among the most characteristic faunal elements of these surfaces, added much to our knowledge of the subject.

It was not until after the Second World War, however, that this biota drew much attention outside of Germany. Papers by Bertrand[4] from the Pyrenees and Marland[5] in Belgium have provided important new information, and additional work is underway in Austria on selected elements of the fauna. It has remained, however, for Vaillant to bring the study of this fauna to full stature.

In some respects the 1956 publication[1] is a summary paper, as it includes many observations which have been noted briefly in and which are pertinent to his 40 or more publications on wet-rock Diptera and Trichoptera. Most of these earlier papers (all dated since 1948!) involve the description of new species, the association of larvae with known or new species of adults, or the study of feeding mechanisms in hygropetric larvae. This more extensive paper redefines the habitat, now, to include not only the steep bare rock surfaces on which a thin film of water runs (Thienemann's hygropetric surfaces) but also the closely associated sediment- and moss-dominated surfaces (hence the term "faune madicole," meaning "fauna inhabiting wet surfaces," equated to a wide sense of the "fauna hygropetrica"). It does not include wet-rock margins or splash zones of larger streams nor does it include the "torrential" steep-rock habitat where depth exceeds a critical 2 mm. at which current becomes overwhelming and the bulk of the inhabitants are unable to be in simultaneous contact with substrate and air. Vaillant describes physical and chemical conditions observed in some 74 sites in southern France, Corsica, and North Africa and proceeds to draw generalizations on the animals found there. American readers may be distressed to see faunal lists serving as central features of some chapters but will be pleased with the organization of all of the material in the lists and in the descriptive sections, the latter including generalizations which are frequently real gems of perception and conciseness. Vaillant has a disturbing tendency to present data in a rather undigested form and then to state conclusions for which the lines of reasoning are not clearly shown, but the reader is likely to be easily convinced that his conclusions must be accepted out of hand, at least until more extensive or more accurate work is done.

For the present this paper is most significant for its generalizations regarding the relations of the very special inhabitants of this discrete habitat to their total environment. As these rather weakly defended and somewhat categorical conclusions are supplanted by more thorough work, however, the lasting contribution will come to be Vaillant's very commendable extension of identifications to the specific level (most workers must be content with identification of aquatic larvae to genus only) and his remarkable expansion of the list of known hygropetric species from 60 to nearly 400. Let us hope that Vaillant's work will not go unnoticed in this country and that it may serve, then, as a stimulus for much-needed work on this interesting and highly instructive fauna.

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[1] Vaillant, F. 1956. Recherches sur la Faune Madicole (Hygropetrique, s. l.) de France, de Corse, et d'Afrique du Nord. Mémoires du Museum National d'Histoire Naturelle (Paris), N.S., Série A, Zoologie, 11: 258 pp.

[2] Thienemann, A. 1909-1911. Eine Beitrag zur Kenntnis der Fauna hygropetrica. Ann. Biol. lacust. (Bruxelles), 4: 53-87.

[3] Feuerborn, H. J., 1933. Die Larven der Psychodiden oder Schmetterlingemacker. Ein Beitrag zur Ökologie der Feuchten. Verhandl. Int. Verein. f. theoret. ang. Limnologie, 1: 181-213.

[4] Bertrand, H., 1948. Les insectes hygropetriques. L'Entomologiste, 4: 86-100.

[5] Marlier, G., 1951. La biologie d'un ruisseau de plaine, l' Smohain. Mém. Inst. roy. Sci. Nat. Belgique, 114.

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THE OCEAN RIVER REFUTED[1]

Since the discovery of the Gulf Stream over four centuries ago, a great amount of both romantic and practical speculation and a much smaller amount of actual investigation has been allotted to it. This book succinctly summaries speculation and investigation, and delineates the course of future research. There is something for everyone here, ecologists included. The first five chapters are devoted to historical aspects, methods of investigation, and qualitative and quantitative descriptions of the Gulf Stream System. The last seven chapters, occupying slightly more than half the volume, discuss the physical phenomena responsible for the observed circulation patterns and their theoretical bases, and a somewhat more detailed analysis of fluctuations and meanders in the Stream's flow than is found in the earlier chapters.

The essence of the exposition is that the Gulf Stream System is actually a boundary condition and an integral part of the entire Atlantic circulation, brought about by the influence of Coriolis force and the earth's rotation upon that circulation. This situation is typified by the westward intensification of oceanic currents. The principles developed here are applicable to all of the world's oceans.

Of particular interest and importance to ecologists and zoogeographers are the observations and deductions involving volume transport, mean flow rates, the formation of eddies, and the sources and sinks of water masses. Much of the type of thinking exemplified by Ekman's ZOOGEOGRAPHY OF THE SEA must ultimately be based upon past and future observations of the types described by Stommel. As a case in point, the discussion of bipolarity of species must take into account Stommel's proposed two-layered circulation of western hemisphere waters; a circulation pattern essentially involving a closed system of water transport between 40°S and 30°N. It should be noted that biologists have attempted to deduce the presence of oceanic currents and transport mechanism through the observation of "biological indicators"; an endeavor largely ignored by physical oceanographers.

Although this book may be read without reference to the theoretical considerations, these considerations and their implications for the study of oceanic circulation naturally constitute the heart of the text. Careful study by even those not fully versed in "higher" mathematics will be amply repaid by an enriched understanding of the methods, viewpoint and theoretical frame of reference of modern physical oceanography. In the last chapter Stommel makes what he calls a "polemical" plea for oceanographic observations to test hypotheses. It seems unlikely that anyone will find fault with such a request.

This is a personal but balanced and objective account which can and should be read by all who are interested in marine science.

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[1] Stommel, Henry. 1958. The Gulf Stream; a physical and dynamical description. University of California Press, Berkeley & Los Angeles; Cambridge University Press, London. xiii + 202 pp., 82 figs., 9 tables. $6.00.

ECOSYSTEMS OF THE WORLD[1]

This is Marston Bates' seventh book. With it he continues his upward climb and outward expansion, bringing to himself an authoritative stature in the field of scientific Natural History (his preferred term) of which the U.S.A. can well be proud. Dr. Bates, Professor of Zoology, University of Michigan, is an entomologist by original training, a mosquit-eer, with an unusual amount (for an American) of foreign experience to his credit. First in Honduras and Guatemala, then around the Caribbean, followed by periods of several years in Albania, Egypt and Colombia, and latterly shorter stints in Micronesia, California and Puerto Rico. Backed by thorough acquaintance with international literature, and with a most commendable resistance to spotlighting his present "territory" (in the animal behavior sense), the book is unquestionably geared to a world audience.

He writes "The material in the book is essentially that of my lectures during the past two years in my undergraduate general education course, "Zoology in Human Affairs." Titles are classic instances of the inadequacy of language as a means of communication. Now if I wrote a book on "Botany in Human Affairs" . . . This book however may be considered a sound and authoritative treatment of the Science of Ecosystems. The science is coming to be called "ecology" by some, for example F. R. Fosberg. It is definitely not the "ecology" of many Americans, which is focused on plant- and plant-and-animal communities and their environments, nor the "ecology" of continental Europe, which is one of several logical subdivisions of their phytosociology. Thus, his "economy of nature" in the title is seen to refer to the integrated aspects of the world about us. Marston Bates is thoroughly holistic in his philosophy, though he does not use the term. He does not factor out isolated elements; he does not erect rigid compartments; he does not classify with the pigeonholing preciseness of a local biota.

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[1] Bates, Marston. 1960. The forest and the sea. A look at the economy of nature and the ecology of man. Random House, New York. 277 pp. $3.95.

Though one can sense an emphasis on animals, nevertheless vegetation, climate, soils and man are all accorded such weight as to reveal a rather remarkable balance as a natural historian, which he would wish to be called.

It is in that part of the subtitle "and the ecology of man" that this book shows a wide divergence from other books of its kind. Dr. Bates accepts man in the scheme of things. Without passing moral judgment or showing emotional fervor, he accepts the effects of man with the same impartiality as he would accept the effects of beaver. He has little sympathy for those who play the game of "let's pretend that man doesn't exist," and who spend their scientific lives nosing into climaxes and virgin states, and believing they have them, even if they haven't.

Although this book was based on college lectures, it bears none of the earmarks of a textbook, in formalism, rigid organization, or pedantry. To the contrary, it flows along with the facility of fiction, with a style that is always interesting, gently humorous, and expressive of great personal modesty, yet packed with information that belies its non-technical terminology. The author is an optimist about mankind (much more so than I am), and this makes for pleasant reading company. There are 16 chapters in the book. The first three are introductory, one with interesting analogies between forest and sea in their vertical dimensions—thus the title of the book. This analogy could be born only in the minds either of tree-climbing amphibians or of human analogues who have indulged, as has Dr. Bates, both in skin-diving and in platform-perching high in tropical trees, even if only to study mosquitoes. The next five chapters discuss the major ecosystems of the world: the open sea, the coral reef, lakes and rivers, tropical rain forest, and those depauperate attenuations of such forest known as woodland, savanna and desert. From there the author discusses the sequence of biological units from cell through individual, population, species and on to the biologic community. He pauses to consider the nature of disease. Chapters 12 and 13 are on individual animal behavior and on social animal behavior. The last 3 chapters involve man and his domesticated animals.

The final chapter, entitled Man's Place in Nature, takes its place with those last-chapters of other books of its kind, where the scientist fits his views into a general philosophy. With frankness, he admits that he "had a great deal of trouble in writing this chapter because I kept getting off on various attempts to derive ethical systems from science or nature, though my topic was the application of ethics to man's relations with nature." He divides his arguments into those that are primarily ethical, esthetic, and utilitarian. "Our anxiety about the future, when we analyze it, turns largely on three related things: the likelihood of continuing warfare, the dizzy rate of human population growth, and the exhaustion of resources. Surely men who can manufacture a moon can learn to stop killing each other; men who can control infectious disease can learn to breed more thoughtfully than guinea pigs; men who can measure the universe can learn to act wisely in handling the materials of the universe. Why are we so pessimistic?" But perhaps he too is pessimistic, for on the next page, in mentioning the nuclear threat, he adds that "It looks as though, as a part of nature, we have become a disease—perhaps a fatal disease. And when the host dies, so does the pathogen." This is indeed an acceptance worthy of a Buddha. Yet he does not fully accept, for "the biosphere is a complex network of interrelations among all the host of living things. Man, in gaining the godlike quality of awareness, has also acquired a godlike responsibility." I am left a bit uncertain as to the responsibilities of biology professors in "zoology in human affairs," and where that responsibility would or should or could be translated into action. Such thoughts though, dangerous ones for many an academic circle, are beyond the scope of this book, which takes its place as a most readable expression of the world's ecosystems, written not only with scholarly soundness, but in a flowing non-technical style that will gain the admiration of students and naturalists, as well as the layman who comes to it unfamiliar with the subject.

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A NATURALISTS' ECOLOGY[1]

This is one of several books published in the past few years which interpret the ecological point of view to the public. May Theilgaard Watts has written a simple, at times poetic, account of some classical ecological concepts and contained them in a volume small enough for even the busiest ecologist to enjoy.

The authoress studied at Chicago under H. C. Cowles and has spent years since observing and interpreting the midwestern landscape in terms of community development. At present on the staff of the Morton Arboretum at Lisle, Illinois, she shares her interpretation with the layman.

The best written chapters in this book are those about the prairie. Mrs. Watts has a feeling for the sweep of the grass-covered landscape and the drama of its origin, exploration and settlement seldom met. Here her documentation is best. In other chapters she sets the deciduous forest scene, vegetationally, and historically, and using a spot or transect—rather than pattern—approach, leads the reader into examples of lake succession, the *Sphagnum* bog and pollen stratigraphy, through a youthful stream valley with attendent gradient of physiographic and vegetational development.

Also described in lucid fashion are some dynamic features of the Lake Michigan dunes, river sand-bar development and vegetational-physiographic features into Wisconsin. Two chapters in the Rocky Mountains—one of them on the tundra in particular—complete her interpretation of the development of natural vegetation.

In the last three chapters Mrs. Watts discusses some recent landscape changes. The first is that about the site of a one room country schoolhouse. She sees some of the changes and infers others from the kind and age of trees present. In another she sets forth again the concept of succession, this time in the development of the city whose origin is a foot path in the forest, leading to a rural lane, a country road, small farm strip development, suburbia, and finally the city; each with its attendent biota. In the last chapter the succession of families on an ample city property is described; each one expressing the mores of its times with the cultigens planted about it.

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[1] Watts, May T. 1957. Reading the landscape. Macmillan Company, New York. x + 230 pp., figs. $4.75.

This little volume is written in a style easily read and understood and is illustrated with line drawings that express pertinent thoughts otherwise unspoken.

One finds few actual compositional errors although some errors in fact are present. The literature cited at the end of each chapter is not well organized and some is out of date. Most of the terminology is simple, some technical, and occasionally the latter is ineptly used. However, ecologists may be glad that Mrs. Watts is teaching resource perception to a generation who will be called upon to evaluate contributions of ecology on the national scientific scene.

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Popular Urban Natural History

John Kieran, well known to the public as a sports and nature writer and a radio and television personality, has recently published a book on A Natural History of New York City.[1] The subtitle reads, "A Personal Report After Fifty Years of Study and Enjoyment of Wildlife Within the Boundaries of Greater New York." Starting as a boy who was born and raised in The Bronx, Kieran spent much of his leisure time throughout his youth and professional career observing nature in his native area. He has made a thorough coverage in the five boroughs which comprise the largest city on the continent of North America. Previously, he published seven books on various aspects of natural history written primarily for young students and the general public. The present volume summarized his field records and observations for more than fifty years in the New York Area. Dr. Kieran is a Field Associate in the Department of Birds at the American Museum of Natural History, and is one of the best known amateur ornithologists.

He opens his book with a brief sketch of the settlement of this area by Europeans and points out the fact that about 40% of the present plant life and an unknown quantity of insect life are also of European origin. Notations of original fauna and flora are quoted from correspondence of some of the early pioneers. Outstanding features of geology, geography, and climate are then pointed out by way of background. Further chapters give a systematic account of the common wildlife known to exist within the city limits in modern times. First described are the marine animals and plants to be found on the more than thirty miles of ocean shoreline. This is followed by chapters on fresh-water life; terrestrial insects; fishes, both marine and fresh-water; amphibians and reptiles. Three chapters are devoted to the lower plants, wildflowers, and the trees and shrubs. Succeeding chapters are devoted to the mammals, the water birds and shore birds, and the upland birds. The concluding chapter traces "The Four Seasons in the City." There is a complete index.

Edwin Way Teale describes this book as, "one long delightful field trip in the company of a charming and erudite companion." For the most part the book is an annotated check-list of flora and fauna. Most groups are considered by taxonomic arrangement and sequence. Dr. Kieran does not hesitate to use Latin names for phyla, classes, and families as well as for species. He spells trivial names with a small letter for plants as well as for animals, thus following the practice of zoologists throughout. In connection with each species mentioned, the author points out something that is particularly characteristic of that organism—its habitat, behavior, food, season present, general abundance, economic importance, relation to man, or some special mark for identification. For the most part, the facts are well known by biologists and naturalists, but are here highlighted for the beginner.

The major contribution of this volume to science is the compilation of a regional flora and fauna which have persisted in spite of extreme urbanization based on records over a long period of continuous observation. While the natural habitats have been and are still being drastically reduced and changed, much of the original plant and animal life remain in the area, but in greatly reduced number. Few will not be surprised at the variety of species still to be found within the city limits. Changes over the past half-century as a result of modified habitat, disturbances, and pollution are frequently pointed out. Introduced species as well as native species are considered, and much of the contents of the book is applicable to a wide area in northeastern United States.

Dr. Kieran terminates his book with the conclusion that, "No man ever will live long enough to learn all there is to know about the wildlife that exists in this great city."

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[1] Kieran, John. 1959. A Natural history of New York City. Houghton Mifflin Company, Boston. xi + 428 pp. Illustrated by Henry Bugbee Kane. $5.75.

A New Series of Technical Papers on the Arctic[1]

The Arctic Institute of North America has published three papers in its new series of Technical Papers. Three additional numbers are expected to appear in the spring of 1960. This series is designed to serve as an outlet for manuscripts that are too long or too restricted in scope for the journal Arctic. The range of subjects is unlimited. The nearest parallel is the Meddelelser om Grønland published in Denmark.

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[1] Johnson, M. W. 1956. The plankton of the Beaufort and Chukchi Sea areas of the Arctic and its relation to the hydrography. Tech. Paper No. 1. Arctic Institute of North America, Montreal, Canada. 32 pp., 11 figs. $0.50.

Manning, T. H., and A. H. Macpherson. 1958. The mammals of Banks Island. Tech. Paper No. 2. 274 pp., 15 figs. $2.00.

Ritchie, J. C. 1959. The vegetation of Northern Manitoba. III. Studies in the Subarctic. Tech. Paper No. 3. 56 pp., 8 figs., 8 plates. $2.00.

The first number by M. W. Johnson describes the numerical abundance and distribution of zooplankton during the summers of 1950, 1951, and 1953 into hitherto unexplored waters of the Arctic Ocean. The flow of water is an important factor in the occurrence and distribution of the organisms.

The second number by Manning and Macpherson is mostly a taxonomic study of the mammals on Banks Island, with observations on abundance and distribution. Fifteen mammals are included, namely, the arctic hare, varying lemming, brown lemming, white whale, bowhead whale, wolf, arctic fox, grizzly bear, polar bear, ermine, wolverine, ringed seal, bearded seal, barren ground caribou, and the muskox.

The third number by Ritchie deals with the composition, structure, environmental relations, and dynamics of the vegetation of a limited area in northeastern Manitoba. Black spruce-lichen open forest occupies low hills and ridges of boulder till while white spruce-lichen open forest is confined to eskers and alluvial deposits. Peat areas are dominated by heath. White birch is common locally along streams and on the long esker extending through the area. Jack pine, aspen, and larch also occur. An annotated list of 257 species of plants is given, 25 of which are arctic-subarctic and the rest boreal or boreal-arctic. In the lichen cover *Stereocaulon paschale* ssp. *evolutoides* is dominant instead of *Cladonia* spp., because the grazing and trampling of caribou repress the latter and favor the more disturbance-tolerant *Stereocaulon.* This paper contributes much information about the poorly known vegetation of the Subarctic Forest near its northern limits. It is a good example of the greater value of a fairly intensive study of a limited area (about 9 by 12 miles) as compared to an extensive examination of a large area.

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Two Journals

Copies have been received by the review editor of two journals of wide interest. One of these, the Internationale Revue der Gesamten Hydrobiologie will be familiar to many as a major journal in its field before the last World War. Publication is resumed with vol. 44 for 1959, with Hubert Caspers, Fritz Gessner, and Arno Wetzel as editors, D. G. Frey as editorial associate in the United States. The journal is international in intent, multilingual (German, English, French) in content. It is published in four issues per year by the VEB Deutscher Verlag der Wissenschaften, Berlin W8, Niederwallstrasse 39, and is priced at DM 30,—per issue.

A distinctive new journal is the Excerpta Botanica, Sectio B, Sociologica, devoted specifically to the publication of bibliographies in vegetation science. Early issues include unannotated bibliographies of vegetation literature of particular countries (Japan, Romania, Germany, Alaska, Palestine, Luxembourg) and of particular topics in plant ecology or the contacts of plant ecology with other fields (root studies in communities, community chorology, soils problems, etc.). Bibliographies are subdivided by a decimal system, and provided with author indexes. The journal is truly international in character, with a world-wide representation of editorial collaborators and contributors. R. Tüxen is editor and H. S. Conard, P. Dansereau, and A. W. Küchler editorial associates in North America. It is published by Gustav Fischer Verlag, Stuttgart, at DM 30,—($7.15) per volume. Readers may note also the continuation of the new series Sarracenia, which includes bibliographic publications, with the title of Weadock and Dansereau below.

Books and Monographs Received for Review

Abrams, Leroy, and Roxana Stinchfield Ferris. 1959. Illustrated flora of the Pacific States. Vol. IV. Bignonias to sunflowers. Stanford University Press, Stanford, Calif. v + 732 pp., 6069 figs., taxon. keys. $17.50.

Bertalanffy, Ludwig von, and Anatol Rapoport (editors). 1960. General systems; yearbook of the Society for General Systems Research. Vol. IV, 1959 (symposium). xxiii + 247 pp., figs. $7.50.

Braungart, Dale C. and Rita Buddeke. 1960. An introduction to animal biology. 5th ed. C. B. Mosby Co., St. Louis. 416 pp., 213 figs., 9 tables. $6.25.

Brockman, C. Frank. 1959. Recreational use of wild lands. McGraw-Hill Book Co., New York, Toronto, London. xii + 346 pp., figs. & tables. $8.50.

Cameron, T. W. M. (editor). 1960. Evolution: its science and doctrine / L'évolution: la science et la doctrine. (symposium) University of Toronto Press, Toronto. xi + 242 pp., figs. $5.00.

Clausen, Robert T. 1959. *Sedum* of the Trans-Mexican belt: an exposition of taxonomic methods. Comstock Publishing Associates (Cornell University Press), Ithaca. x + 380 pp., 81 figs., tables. $7.75.

***Christophers, S. Rickard.** 1960. *Aedes aegypti* (L.), the yellow fever mosquito: its life history, bionomics and structure. Cambridge University Press, Cambridge & New York. xii + 739 pp., 86 figs., 50 tables. $14.50.

Crispens, Charles G., Jr. 1960. Quails and partridges of North America: a bibliography. University of Washington Press, Seattle. xii + 125 pp. $3.25.

Curry-Lindahl, Kai (editor). 1959. Våra fåglar i Norden. (Our birds in the North) (symposium). Bokförlaget Natur och Kultur, Stockholm. 557 pp., num. figs., color plates.

Dansereau, Pierre. 1959. Phytogeographia Laurentiana. I. Introduction et méthodologie. II. The principal plant associations of the Saint Lawrence Valley. Contributions de l'Institut Botanique de l'Université de Montréal Nos. **74:** 1-18, **75:** 1-147, figs. & tables.

Esau, Katherine. 1960. Anatomy of seed plants. John Wiley & Sons, Inc., New York & London. xvi + 376 pp., figs. $6.95.

***Horsfall, J. G. and A. E. Dimond** (editors). 1960. Plant pathology; an advanced treatise. Vol. II. The pathogen. (symposium) Academic Press, New York & London. xiv + 715 pp., figs. $22.00.

***Hynes, H. B. N.** 1960. The biology of polluted waters. Liverpool University Press, Liverpool. xiv + 202 pp., 22 figs., 11 tables. 25s., $3.50.

Illinois Department of Registration and Education, Division of Industrial Planning and Development. 1960. Atlas of Illinois Resources, Section 3: Forest, wildlife, and recreational resources. 46 pp., 16 color maps.

Jones, William O. 1959. Manioc in Africa. Stanford University Press, Stanford. xiv + 315 pp., tables & maps. $6.75.

Kramer, Paul J. and Theodore T. Kozlowski. 1960. Physiology of trees. McGraw-Hill Book Co., Inc., New York, Toronto, London. xiii + 642 pp., figs. & tables. $12.50.

Kroeber, A. L. & S. A. Barrett. 1960. Fishing among the Indians of northwestern California. Anthropological Records vol. **21**, no. 1, 210 pp., 49 figs., 74 maps, 32 plates.

Kusnezow, S. I. 1959. Die Rolle der Mikroorganismen im Stoffkreislauf der Seen. Transl. from Russian by A. Pochman. VEB Deutscher Verlag der Wissenshaften, Berlin. x + 301 pp., 77 figs. DM 36,—, $8.60.

Lötschert, Wilhelm. 1959. Vegetation und Standortsklima in El Salvador; eine pflanzengeographisch-ökologische Studie. Botanische Studien Heft **10:** viii + 88 pp., 38 figs. & 20 plates. DM 14, 30, $3.40. VEB Gustav Fischer Verlag, Jena.

***Meyerriecks, Andrew J.** 1960. Comparative breeding behavior of four species of North American herons. Publications of the Nuttall Ornithological Club, no. **2**, viii + 158 pp., 39 figs. 15 plates, 21 tables. $2.00 paper, $3.00 cloth (Massachusetts Audubon Society, Drumlin Farm, South Lincoln, Mass.).

Mohlenbrock, Robert H. and John W. Voigt. 1959. A flora of southern Illinois. Southern Illinois Uniersity Press, Carbondale. ix + 390 pp., 67 figs., taxon. keys. $7.50.

Morello, Jorge. 1958. La provincia fitogeografica del Monte. (Engl. summ., Phytogeographic province of Monte, Patagonia) Opera Lilloana **2**, 155 pp., 59 figs., 58 plates. Universidad Nacional del Tucuman, Tucuman.

Mozley, Alan. 1960. Consequences of disturbance; the pest situation examined. H. K. Lewis & Co., London. x + 61 pp. 9s., $1.30.

Murie, Olaus J. 1959. Fauna of the Aleutian Islands and Alaska Peninsula (with notes on invertebrates and fishes collected in the Aleutians, 1936-38, by Victor B. Scheffer). North American Fauna no. **61**, xiii + 406 pp., 69 figs. U. S. Fish and Wildlife Service, Washington. $1.25.

Nelson, John B., consulting editor, and **D. G. ff. Edward,** conference chairman. 1960. Biology of the Pleuropneumonialike organisms. (symposium) Annals of the New York Academy of Sciences, Vol. **79**, art. 10, pp. 305-758, figs. & tables. $5.00.

***Nicol, J. A. Colin.** 1960. The biology of marine animals. Interscience Publishers, London & New York. xi + 707 pp., figs. & tables. $14.00.

Overgaard Nielsen, C., and Bent Christensen. 1959. The Enchytraeidae; critical revision and taxonomy of European species. Natura Jutlandica, vol. **8-9.** 160 pp., 177 figs., 11 tables. Naturhistorisk Museum, Aarhus.

Pacific Science Association. 1958. Climate, vegetation, and rational land utilization in the humid tropics. (symposium, F. R. Fosberg, chairman). Proceedings of the Ninth Pacific Science Congress, vol. **20**, vi. + 169 pp., figs. & tables. Secretariat, Ninth Pacific Science Congress, Bangkok.

Porter, C. L. 1959. Taxonomy of flowering plants. W. H. Freeman & Co., San Francisco & London. xii + 452 pp., 600 figs. $6.75.

Rabotnov, T. A. 1950. Life-cycle of perennial grass vegetation in meadows (In Russian). Works of the V. L. Komarov Botanical Institute, Academy of Science of USSR, Series III (Geobotanica), issue **6**, 204 pp., 8 figs., 43 tables.

Ramensky, L. G., with O. N. Chizhikov, I. A. Tsatsenkin, and N. A. Antipin. 1956. Ecological evaluation of nutrient fertilization of vegetive cover (In Russian). State Publications of Rural Economy Literature, Moscow. 472 pp., 9 figs., tables.

Ray, Dixy Lee (editor). 1959. Marine boring and fouling organisms. (symposium) University of Washington Press, Seattle. xii + 540 pp., figs. & tables. $8.50.

Schoeller, H. 1959. Arid zone hydrology; recent developments. Arid Zone Research no. **12**, 125 pp., 29 figs., tables. 8,75 NF, $2.50. UNESCO, Paris.

Simpson, George Gaylord, Anne Roe, and Richard C. Lewontin. 1960. Quantitative zoology. Revised edition. Harcourt, Brace & Co., New York. vii + 440 pp., 64 figs., tables.

***Stanković, Siniša.** 1960. The Balkan Lake Ohrid and its living world. Monographiae Biologicae, vol. **9**, 356 pp., 101 figs. Uitgeverij Dr. W. Junk, Den Haag. *f* 35.—.

Waterman, Talbot H. (editor) 1960. The physiology of Crustacea. Vol. I. Metabolism and growth. (symposium) Academic Press, New York and London. xvii + 670 pp., figs. & tables. $22.00.

***Waters, Rolland H., D. A. Rethlingshafer, and Willard E. Caldwell.** (editors) 1960. Principles of comparative psychology. (symposium) McGraw-Hill Book Co., New York, Toronto, London. ix + 453 pp., figs. $7.95.

Weadock, Virginia, and Pierre Dansereau. 1960. The SIGMA papers; a short history and a bibliographic review. Sarracenia, no. **3**, 47 pp. Institut Botanique, Université de Montréal, Montréal.

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* Assigned for review.